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# PLANT LIFE AND EVOLUTION

BY

DOUGLAS HOUGHTON CAMPBELL

Professor of Botany in Leland Stanford Junior University



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# **PLANT LIFE AND EVOLUTION**



# PLANT LIFE AND EVOLUTION

## CHAPTER I

### INTRODUCTION

**S**PECULATIONS concerning the origin of life upon the earth, and the nature of the primeval organisms from which are descended existing plants and animals must always have for the biologist an irresistible attraction. When we realize the extraordinary development of modern experimental biology, it would be rash to say that the problem of the origin of life is insoluble, but it must be admitted that its solution does not seem to lie in the immediate future.

**Life and Its Origin.**—All living things are built up of chemical elements that also occur in an “inorganic” condition; and the nature of the combinations of these elements into the substances that make up living matter, and the functions or “life processes” associated with this living matter, are the problems with which the biologist has to deal. Whether all of these “vital” phenomena are reducible to terms of physics and chemistry, may perhaps be open to question; but as yet we have no

positive evidence that this is not the case, and all experimental work must necessarily be based upon the assumption that living matter is subject to the same laws that govern inorganic bodies.

So far as can be demonstrated, all manifestation of life is indissolubly associated with certain extremely complex "protein" substances which never occur except in living bodies, and which are the basis of the protoplasm, or living substance, of all plants and animals.

The evidence as to the possibility of spontaneous generation at the present time is entirely negative. All of the alleged successful experiments in this direction have been shown to be the result of errors, and as yet no successful attempts have been made to produce living matter by artificial means. So far as we know at the present time, all living things arise from preëxisting ones by some form of reproduction. It is, however, the general belief of biologists, that at some remote period living matter arose from inorganic elements. The theory that living germs were brought to the earth from somewhere in space is not generally accepted; and the criticism has been made of this view that, after all, it does not explain the *origin* of life, but merely the advent of life upon the earth.

Probably the most important advance made in recent years towards an understanding of the nature of the most primitive forms of life, has resulted from the study of certain bacteria, which both

structurally and physiologically must be regarded as the simplest organisms of which we have any knowledge. Especially are we indebted to the researches of the Russian investigator, Winogradsky, for information regarding these important little organisms. These bacteria possess the remarkable power of assimilating the free nitrogen of the atmosphere, and some of them, like the higher green plants, can decompose  $\text{CO}_2$ ,\* and they are thus able to live quite independently of any organic food, a condition of things hitherto supposed to be confined to plants possessing the characteristic green pigment chlorophyll. Unlike the green plants the assimilations of  $\text{CO}_2$  in these bacteria is not dependent upon light; i.e., it is not a process of "photosynthesis."

We have then, in these nitrogen bacteria, organisms of the simplest structure so far as we can judge, although their excessively minute size may account for the failure to demonstrate any definite cell structure. In their ability to assimilate such simple and common substances as nitrogen and  $\text{CO}_2$  they may very well be assumed to approximate the earliest forms of life that appeared upon the earth. It is reasonable to suppose that these primitive organisms, like the nitrogen bacteria, were able to assimilate free nitrogen,  $\text{CO}_2$ , and water, which yield the most important elements of the proto-

\* Carbonic acid gas. The reader is urgently invited to fall in with the convention which now accepts this abbreviation quite generally in non-technical writing.

plasm. What were the sources of energy for these assimilation processes, of course we cannot tell, since the requisite energy may have been of various kinds and derived from various sources,—light, heat, or chemical energy, as any of these forms of energy might very well serve the same purpose. Thus the assimilation of  $\text{CO}_2$  by the green plants requires light for its accomplishment, but the nitrogen bacteria are able to assimilate  $\text{CO}_2$  in the absence of light, probably through some form of chemical energy.

When life first appeared upon the earth the temperature was presumably very much higher than at present, and chemical activity would probably have been more active. It has been supposed also that  $\text{CO}_2$  was more abundant in the atmosphere than at the present time. Inasmuch as the assimilation of  $\text{CO}_2$  by the nitrogen bacteria is independent of light, it is not necessary to assume that this assimilation in the earliest forms of life was photosynthetic; but what agency transformed the presumably highly unstable and complex inorganic compounds, which antedated the first living things, into living protoplasm with its power of assimilation and growth, we do not know. It may be that further experimental work on these simple living things, the nitrogen bacteria, may furnish the key to the mystery of the origin of life.

The distinguished botanist, Pfeffer, says: "It remains uncertain whether the conditions now exist-

ing on our globe are such as to permit a re-creation of life, or whether the necessary conditions were presented once, and by a special sequence of events such as we can never hope to reproduce. The particular combination of causes, to which the creation of life was possibly due, may have existed only as the earth cooled from its original incandescent condition and perhaps thereby caused certain essential preliminary stages in the production of living substance to arise."

**Protoplasm.**—All manifestations of life are directly associated with living protoplasm. When, however, we attempt to define protoplasm we meet with serious difficulties. We know that this viscid, more or less granular matter, which constitutes the living part of all cells, is an enormously complex substance. Protoplasm is in no sense a definite homogeneous chemical compound, but it is a mixture of very many presumably heterogeneous units, which in themselves may be of great complexity. Of the real nature of the units making up the protoplasmic body of the cell we have very little certain knowledge. Various names,—“biophores,” “gemmules,” “micellæ,” etc., have been proposed for these assumed units, but whatever may be their structure, they lie far beyond the reach of our best microscopes, and it will hardly be profitable here to dwell upon the various theories that try to explain the ultimate structure of the protoplasm.

Any chemical analysis of protoplasm must be only

approximate, since an essential condition of active protoplasm is its great instability. As the result of the activity within the protoplasm, new substances are constantly being formed, some being constructive elements of the growing protoplasm, others excretions which cannot be considered as truly a part of the living protoplasm. Moreover, there may be unassimilated food products from without. Nevertheless, in a general way the essential chemical composition may be determined, and we know that the protoplasm of all organisms contains very much the same chemical elements. The chemical elements which are absolutely essential are comparatively few, the most important being oxygen, hydrogen, carbon, and nitrogen, which compose the greater part of the protoplasm; but sulphur, phosphorus, potassium, calcium, and iron are never absent from normal green plants. Of course it must be assumed that the proportion and arrangement of these are different in different organisms.

There is always present in active protoplasm a large percentage of water which is necessary to put the protoplasm in the semi-fluid, viscous condition essential for its activity. Moreover, the water is a solvent for most of the food elements needed for the growth of the protoplasm. The water thus serves a twofold purpose; first as a mechanical agent putting the protoplasm in the labile condition necessary for manifesting activity; and second, as a means of transport of food in the form of solu-

tions. Through the decomposition of water, plants also obtain material for the manufacture of organic matter. While the presence of the water is essential for protoplasmic activity, its withdrawal does not necessarily kill the protoplasm. In plants, especially, certain structures like spores and seeds may be deprived as completely as possible of all traces of free water without at all injuring the vitality of the protoplasm, which quickly resumes its activity when the necessary water is supplied. While it is true that the chemical composition of all protoplasm is much the same, it is equally clear that it cannot be absolutely identical for any two organisms. The enormous complexity of its constitution offers room for infinite variations in both the composition and arrangement of the ultimate protoplasmic units; and it is reasonable to suppose that the inherent variability of all organisms is to be traced back finally to these inevitable variations in the protoplasm of which they are built up.

**The Cell.**—With few exceptions the protoplasm is segregated in definite bodies or cells. In all but the very lowest plants the protoplasmic body of the cell—the “protoplast”—always contains a well-organized nucleus like that found in the cells of animals. There are also in all of the green cells definite bodies, chromatophores, in which is contained the chlorophyll. Both the nucleus and chromatophores always arise by division and are never formed anew in the protoplasm. Other

bodies may be sometimes recognized, such as the "microsomes," and there is every reason to look upon the protoplast as an organism, made up of permanent parts or organs, of which only a few, like the chromosomes of the nucleus, and the chromatophores, are readily demonstrated.

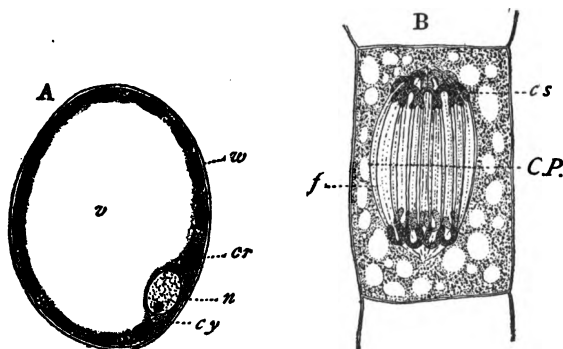


FIG. 1

A—Diagram showing the parts of a typical plant cell—*w*, cell wall; *cy*, cytoplasm; *n*, nucleus; *cr*, chromatophores; *v*, central vacuole, filled with watery cell-sap.

B—A cell in process of division—*cs*, chromosomes; *C.P.*, beginning of the division-wall; *f*, spindle-fibers.

What the nature of the invisible organs—"bio-phores," "pangenes," etc.—is, of course, at the present can only be conjectured, but it is probable that they are of very many kinds and that they always multiply by division as do the nucleus and chromatophores. Thus there are distributed to the daughter cells after each cell division similar elements which insure a great degree of similarity and

determine the quality of the cell. As it is not conceivable that there should be an exact distribution of the constituents of the cell in cell division, it necessarily follows that no two cells can be exactly alike, and these differences may be increased by subsequent changes in the cells during the development of the organism. Although it is probable that the invisible units that make up the protoplasm are of many kinds, it is also pretty certain that the differences between two protoplasts may be due not so much to diversity in the actual structure of the particles of each, as to a different grouping of the particles, involving a different reaction toward the many stimuli to which the protoplasmic structures are subjected in the course of their development.

**Plants and Animals.**—While all the higher organisms may be readily assigned to either the plant or animal kingdoms, this is not the case with many of the simplest forms of life, and the division of living things into plants and animals is more or less arbitrary. The living cells of all organisms are composed of protoplasm, and all of them perform the same life functions,—i.e., they respire, feed, grow, and reproduce, and these functions are very similar in all living things. The differences between plants and animals are largely physiological ones, and are by no means universal. Typical plants—i.e., those that possess chlorophyll—can live entirely upon inorganic food, and are able to utilize the radiant energy of sunlight for the manufacture

from  $\text{CO}_2$  and water of simple organic compounds.

The ability to feed entirely upon inorganic matter is not, however, in all cases dependent upon light. We have already seen that certain bacteria can do this in the absence of light, probably through the agency of some form of chemical energy. Animals, so far as we know, are absolutely dependent upon organic food for their existence, feeding directly or indirectly upon plants. Where chlorophyll is present in animals, as for instance in the green hydra and fresh-water sponges, it has been shown that the green color is due to the presence of minute green algæ which live within the tissues of their host. Of unicellular animals, it has been claimed that a species of *Vorticella* contains chlorophyll, and a common flagellate organism *Euglena*, which is structurally more like an animal than a plant, and is often considered to be a true animal, contains abundant chlorophyll and is undoubtedly capable of photosynthesis.

**Plants the Manufacturers of Organic Matter.—**

Plants being the manufacturers of all organic food, their importance in the economy of nature is at once evident. Without them all animal life would necessarily soon cease. While the green plants take the first place in the manufacture of organic compounds, it must be remembered that the lowest of all plants, the bacteria, are also indispensable in maintaining the circulation of materials necessary

for the nutrition of all higher organisms. This is accomplished in two ways; first, by the assimilation of free nitrogen and the changing of certain nitrogeous constituents of the soil into forms that can be used by the higher plants; and second, through the decomposition of dead organic matter which is thus put in such a form that it can again be used by green plants. All organisms in the course of their development give off waste products which ultimately serve as food for other organisms. Most of these waste products except  $\text{CO}_2$  and water are not directly available for the food of green plants, but must first be acted upon by bacteria. The bacteria, also, as has been indicated, are the principal agents by which the dead tissues of plants and animals are decomposed so that they are again available as food for the higher plants. There are, however, many undoubted plants such as the fungi—i.e., molds, mildews, rusts, mushrooms, etc.—as well as certain flowering plants that are destitute of chlorophyll, like the dodder and Indian pipe, which require organic food just as animals do.

We may say, however, that the typical plant contains chlorophyll and has the power of photosynthesis; that is, can use the energy of sunlight for the manufacture of organic compounds from  $\text{CO}_2$  and water. Animals are not provided with chlorophyll and are entirely dependent upon organic food for their existence. Animals are as a rule much more mobile than are plants, and this is correlated

with the different method of their nutrition. With few exceptions the cells of plants are surrounded by a firm membrane which precludes motion except where there are openings for the protrusion of the protoplasm, a condition which sometimes occurs in unicellular plants or those composed of a small number of cells. The tissues of the higher plants, made up of these firm walled cells, are capable of only a limited amount of motion. In animals the cell-wall is much less evident in active tissues, and is often not developed at all, thus allowing a much greater degree of mobility in the cells than is the case in plant tissues.

**Plants Immobile Organisms.**—The plant having a constantly renewed food supply,  $\text{CO}_2$  from the atmosphere, and water and mineral compounds from the earth, has no need to move from its position; while the animal, obliged to move from place to place in search of food, must be provided with special organs of locomotion. If, however, an animal is so placed that it is provided with a constant supply of food within its reach, it may often show a plant-like immobility. This is seen in the case of many parasites, and in such aquatic animals as sponges, hydroids, and corals, which in their adult condition sometimes curiously mimic vegetable forms very closely, hence their old name of “zoöphytes.” Many mollusks, like the oyster and mussel, are also fixed in their adult condition. Such stationary animals have developed ciliated organs

which create currents in the water, carrying with them the organisms needed for food. These fixed animals, at some stage in their development, must provide for dispersing themselves, and very commonly the larvæ are actively motile. In other cases it is the adult which is active, as with many insect parasites, the larvæ being incapable of moving away from their host. The same necessity for the distribution of the species is seen in plants, whose reproductive parts show many methods of dispersal. In the lower plants, freely motile reproductive cells are common. In the higher plants, the distribution of the reproductive parts—spores, seeds, etc.—is usually passive, but these structures are often modified so as to facilitate the distribution by special means, such as dispersal by the wind of many winged seeds and fruits, or the development of hooks by which these adhere to animals and are thus transported.

The fixed position of plants involves a high degree of adaptability, and they show a capacity for growth and regeneration that can hardly be matched in animals. The most highly specialized plants are far less individualized than the majority of animals; indeed it is not always easy to limit the individual, as most plants may perhaps be looked upon rather as a colony of united units than as a single individual. Not only are the cells of plants less various than those of animals, but there may be also an almost unlimited repetition of similar organs.

We have but to compare a tree like the oak, for example, with a highly specialized animal like the horse. The former may live for centuries, producing each year thousands of leafy twigs and flowers, each like its neighbors. The complexity of the plant is due to the multiplication of similar organs rather than to a great number of different parts. The animal is sharply individualized, its different organs being absolutely definite in number and position with only a limited power of regeneration. It has a very limited and definite period of growth, with a correspondingly brief life-span.

**Regeneration in Plants.**—The power of regeneration in the higher animals is very limited. A wound may heal, and such organs as nails, feathers, and hair may be replaced, and in some lower vertebrates even a whole limb or tail may be regenerated. But in the higher forms of animals, the regeneration of whole individuals, except sexually, never occurs. In plants, on the other hand, even in the highest ones, the regeneration of the whole individual from almost any member of the body is possible, and this fact is constantly taken advantage of in the artificial propagation of plants by cuttings, grafts, etc. In some cases a fragment of a leaf or root is enough for the development of a complete plant, and in many of the lower plants, a single cell is sufficient. Plants also may show a regular periodic regeneration of certain organs, such as leaves and flowers, which are short-lived and

perish after they have served their purpose and are replaced each season by entirely new formations. While this development of temporary organs may occur in animals, i.e., the moulting of special plumes in the breeding season of birds, the seasonal development of the horns of deer, the summer and winter coats of many animals, etc., these organs are not essential ones, and the structures in which they develop are permanent, as for instance the feather and the hair-papillæ.

**Plants Less Specialized than Animals.**—There is, in short, far less difference between the higher and lower forms among plants than is the case among animals. The relative simplicity of even the highest plants perhaps accounts for their greater plasticity. Their immobile condition makes it necessary for them to be able to endure the changes of temperature, light, moisture to which they may be subjected, as they have no power to move away in search of more favorable conditions after they once become fixed. Many plants show an extraordinary adaptability for growing under extremely diverse conditions, and may be so changed as to be scarcely recognized as the same species. Thus a tree which grows to a large size in a sheltered valley, may survive near the timber line on a lofty mountain, as a prostrate shrub, rising but a few inches from the ground; or a weed, growing tall and rank in a damp and shady fence corner, may shrink to a tiny herb with minute leaves and thin wiry stems, when grow-

ing in a sun-baked, hard-trodden path; and yet they will succeed in flowering and maturing their seeds under these adverse conditions. This adaptability of plants and the readiness with which they respond to changes in environment make them especially suited to experiments, and in many ways they are therefore easier to study than are most animals. It is not strange then that they should have been made the subject of many experiments bearing on the question of the factors concerned in organic evolution and the origin of species.

## CHAPTER II

### FACTORS IN EVOLUTION

**P**ROFESSOR H. F. OSBORN has recently enunciated the law of four inseparable factors that may be denominated the primary processes of evolution. He says: "The life and evolution of organisms continuously center around the processes which we term heredity, ontogeny, environment, and selection. These have been inseparable and interacting from the beginning; a change introduced or initiated through any one of these factors causes a change in all."

#### HEREDITY

**Heredity.**—The transmission of like characteristics from parent to offspring is a sufficiently familiar phenomenon, but the factors directly concerned with this are by no means clearly understood. It is inconceivable that under any circumstances an acorn should produce anything but an oak, or that the offspring of a dog should be anything but a dog; but *why* the germ cell of a specific organism should always follow the same course of

development is not so obvious. In the majority of animals new individuals can arise only from the specialized reproductive cells, and as a rule the formation of a new individual is the result of the fusion of two gametes, or sexual cells, the ovum and spermatozoön, which are markedly different from the somatic cells, i.e., the cells that compose the various tissues of the body. In very many plants there is a similar development of sexual cells, and the process of fertilization is essentially the same as in animals; but most plants also multiply asexually, and not a few plants are known in which this is the only method of propagation. Hence we must remember that hereditary characteristics are not transmitted by sexual cells alone. The plants whose propagation is strictly asexual are not only the lowest forms, like the bacteria, but also a good many algæ and fungi, some of them plants of large size and complex structure. Among cultivated plants are many which rarely or never produce perfect seeds and are always propagated by division. The banana, pineapple, breadfruit, and sugar cane are examples of these, and the many varieties of domesticated plants which have arisen in cultivation transmit their characters in a purely non-sexual way. Bud variation is a not infrequent phenomenon, and such variations are readily perpetuated by cuttings or grafts.

**Asexual Reproduction in Plants.**—No cases are known among the vascular plants, i.e., ferns and

seed plants, where a single somatic cell can develop into a new plant; but in some liverworts this is possible, and among the algæ it is a common phenomenon. These asexual reproductive cells in the latter plants are often free swimming "zoöspores." This great regenerative power shown by the vegetative cells of plants is entirely in harmony with the generally lower degree of specialization shown by plants when compared with animals.

The capacity of reproducing from a single cell, the egg, the whole of an exceedingly complex organism, shown especially in the case of the higher animals, has led to much speculation concerning the actual structures that are the basis of hereditary transmission. The theory of a special "germ-plasm," "biophores," "pangenes," etc., which are the bearers of hereditary characters, has been the subject of many ingenious speculations, none of which, however, is capable of actual demonstration. The phenomena of nuclear division point to the chromosomes as being important agents in heredity, but it is not likely that they are the sole bearers of hereditary characters.

**The Agents in Heredity.**—The immensely complex structure of the protoplast permits of infinite variation in the arrangement of its constituents, and whether or not we assume the presence of special permanent determining structural units such as the "determinants" of Weismann, it is evident that the germ cells of every organism possess their own in-

dividual characters, and these characters must be transmitted through cell division to all of the descendants of the germ cell. The ultimate structure of the germ cells of two species being different, it follows that their responses to the various stimuli to which they are subjected during the development of the embryo will also differ, and moreover the conditions to which the developing embryos of any two species are exposed also may be supposed to differ to a greater or less degree.

In a general way we may say that the degree of difference between two organisms is determined, first, by structural differences of the germ cells, and secondly by the different conditions to which the germ cell is exposed in the course of its normal development. Given two identical germ cells, subject to identical conditions throughout their development, and the result must be two identical organisms. Pfeffer very properly lays stress upon the importance of the physiological factors in heredity as distinguished from purely structural ones, and this view has also been expounded by Peirce, Farmer, and other physiologists. The chemical and physical stimuli to which the protoplasmic units are constantly subjected are quite as potent in determining the character of the resulting structure as is the mere chemical composition of the different protoplasmic units of which the germ cell is composed. It does not, however, follow that the offspring must be an exact

duplicate of the parent, and we know that it always departs more or less from the parental type. These departures from the type may be very marked, and it is not unlikely that these changes may be so great sometimes as to pass beyond the limits of the so-called fluctuating variations that are common to all species, and in such cases there arise so-called "mutations," which may be permanent in case crossing is prevented. Such sudden or discontinuous variations are assumed by some biologists to be the all-important cause of the formation of new species. This view is especially held by De Vries, whose studies in mutation have lately attracted so much attention. As to the causes of these mutations, however, we are very much in the dark, and much more evidence is needed before it will be safe to assume that mutations alone are the real origins of new species.

That the constitution of all the germ cells of a given species is essentially the same, and that in the normal course of development the growing organism is subject to the same conditions, will account for the main facts of heredity, without assuming any special germ-plasm or "formative materials" corresponding to special organs. The phenomena of regeneration in plants all point to the correctness of this view.

There must be inevitably a greater or less difference between the cells resulting from any cell division, and these differences must be reflected in the

individual differences existing between any two members of the same species. The germ cells, as a rule, are so situated as to be less subject to external influences, and are much more stable than the ordinary vegetative or somatic cells. How far they may be affected by external conditions, and to what extent, if any, changes thus affected are transmitted by heredity, is one of the questions which has been very much discussed, but about which there is really very little positive evidence.

### ONTOGENY

**Ontogenetic Variations.**—Every organism passes through a more or less extensive series of changes during its development from the germ to maturity. In the course of its life-history, or “ontogeny,” individual variations occur, some of which can be attributed to the environment, while others are apparently innate. It is these ontogenetic variations which distinguish the innumerable individuals belonging to a species. We may examine a hundred seedlings, reared apparently under the same conditions, and no two will be exactly alike. The biologist has no more difficult problem than that of determining the causes of these variations. While in many cases the effects of extrinsic factors can be easily demonstrated, as for instance dwarfing caused by insufficient nutrition, more often the variations seem to be innate differences which begin in

the germ, and are due to more or less marked divergencies in the very constitution of the germ cells, and these differences are reflected in the organisms developed from them. How far these ontogenetic variations are transmissible is hard to determine, but it seems reasonable to suppose that they are not without their effect in determining the future history of the race.

### ENVIRONMENT

**Irritability.**—Protoplasm is distinguished by the remarkable property of irritability, i.e., the power of reacting to various external stimuli, such as light, heat, electric currents, mechanical shocks, etc., as well as to the so-called automatic stimuli, or those arising within the protoplasm itself. These external stimuli constitute an important part of the environment which is so powerful a factor in the shaping of every organism. Were the protoplasm absolutely uniform in all cases and the environment constant, there would necessarily be no change, and evolution could obviously not proceed. But by their very nature the protoplasts of no two cells can be exactly alike in structure, and there must be a corresponding degree of variability also in their behavior towards any stimuli. Moreover, the environment cannot remain absolutely constant but must change to a greater or less degree. Inherent variability in the structure of the protoplast, and the

inevitable fluctuations in the environment may be considered as the fundamental causes of that variation which is the beginning of any line of evolution.

**The Effects of Stimuli.**—As we are very ignorant of the physical structure of protoplasm we can only guess at the reactions that are developed within it as the results of various stimuli. While we speak of the formative effects of light, heat, and other extrinsic factors, it is extremely unlikely that the effects of these are immediate. As the results of their action certain effects finally develop; but how far these are the direct result of the evident stimuli, and how far they are caused by others not so apparent, we have no means of judging. It is certain that a single, apparently insignificant stimulus may set in motion a chain of reactions which result in far-reaching effects. We might compare this to a mine, which may be fired by a single spark, or by a percussion cap, the final result of the explosion being the annihilation of a whole town. A fern-spore lies dormant in a state of physiological equilibrium; it is placed in water, and immediately there is set up a series of reactions which result in its germination and final development into the mature plant. Light or heat may be the stimulus which is necessary, but once inaugurated the succession of reactions must follow. The fertilization of the egg and its subsequent development into the animal offers an equally striking instance of the far-reaching results of an apparently slight stimulus.

**Cumulative Effects of Stimuli.**—It has often been demonstrated that the effects of stimuli may be cumulative, and that when a stimulus is repeated at short intervals the response to this may be very different in the later cases of stimulation. Thus Jennings, in his important studies on the reactions of the Infusoria, has shown that they may become habituated to a stimulus, and fail to respond to it again after it has been repeated several times. It would appear that the “physiological state” of the cell has changed as the result of the stimulus, and in a very suggestive recent address by Prof. F. Darwin, he brings forward the theory that this permanence of the effects of stimulation upon the protoplasm, or “memory” as he boldly puts it, is perhaps the most potent of all causes in determining the course of evolution in the development of an organism.

**Experiments with Slime-molds.**—Where protoplasm occurs in large masses, as it does in those remarkable organisms the slime-molds, its reaction to various stimuli is easily demonstrated. Exposed to strong light, the slimy mass or “plasmodium” will seek shelter in the crevices of the rotten log on which it is growing or will hide under the masses of dead leaves or tan bark which may serve it for food. The movements will be accelerated by an increase of temperature; withdrawal of moisture will cause a contraction or even make it assume a quiescent stage; and in short the sensitive mass of

living slime responds promptly to the various stimuli which may be brought to bear upon it.

As a rule, however, the protoplasm of plants is shut up in closed cells, but the living protoplast included within the cells often shows evident movements, and may be seen to react toward stimuli in the same way as the naked plasmodium of the slime-mold. If the green corpuscles or chloroplasts are present in the cells, these may be seen to shift their position under the influence of light, and the protoplasmic movements which are very common within the cells are affected readily by different stimuli. When the protoplasm escapes from the cell, as it sometimes does in the reproductive cells, especially among the lower plants, these motile cells usually react promptly to various stimuli. Thus zoöspores will usually swim towards the source of light, and the spermatozoids of ferns are strongly attracted by the salts of malic acid.

**Reactions of Multicellular Organs, Due to Irritability of Protoplasm.**—The movements and other indications of response to stimuli, shown by the multicellular organs of the higher plants, are undoubtedly induced primarily by the reaction of the protoplasm within their cells. It has been shown that in many plants there is a direct communication between the protoplasts of neighboring cells, due to the penetration of the cell walls by the fine threads of protoplasm, and it is highly probable that in this way the effects of stimuli may be propagated

from cell to cell, somewhat as is the case in animals, where there is a specialized nervous system. Our knowledge of the transmission of stimuli in plants, however, is very far from complete. Of a very different nature are certain movements which are purely mechanical. Thus the twisting of the awns in many grasses, or in the alfilaria (*Erodium*), or the movements of the "elaters" in *Equisetum* or the liverworts, are purely mechanical movements due to the absorption of water.

**Unicellular Plants.**—The simplest green plants consist of a single cell, which may be motile, but usually is non-motile and most often globular or oval in form. The cell is usually enclosed in a membrane of cellulose. The protoplast contains a nucleus and one or more green corpuscles or chromatophores. Such a simple green cell is able to perform all the essential life functions. These low plants are mostly aquatic, and with the water absorbed from the medium surrounding them, there are taken into the cell in solution the various food constituents which the cell needs for its development. Oxygen is absorbed for the respiratory process, and in the chromatophores the  $\text{CO}_2$  dissolved in the water is decomposed and united with the hydrogen and oxygen derived from the decomposition of water. Such green cells exposed to the light for a short time will show in the chromatophores the first visible evidence of their assimilation, or photosynthesis, in the form of starch, this carbon

assimilation being accompanied by the evolution of free oxygen. The cell increases in size until it reaches its full development and then by division two cells are formed, which constitute new individuals.

Such simple unicellular plants react promptly to the environment. Deprived of light, photosynthesis at once ceases; changes in temperature materially effect the activity of nutrition and growth which only can be maintained within certain often decidedly small limits; should the temperature of the water in which the plant is growing be raised above a certain point, death will result. Most of the lower plants are much more resistant to low temperatures and may often be frozen solid without injury. Withdrawal of water does not necessarily destroy the plant. Many of them simply become dormant, remaining inert so long as they are dry, but absorbing water quickly when moistened, and soon resuming activity. Retention of moisture is often facilitated by the gelatinous character of their walls, which hold water very tenaciously.

**Most Plants are Multicellular.**—While there are many plants which are unicellular and some of these are quite highly specialized, the greater number of plants are multicellular. The simplest multicellular plants are filamentous algæ, rows of often slightly coherent and quite uniform cells. Such a plant might be considered as a chain of unicellular individuals rather than a multicellular individual, and

sometimes a single cell may separate and give rise immediately to a new filament. Many of these lower filamentous algæ may under certain conditions assume a unicellular condition and this may be induced artificially, this unicellular stage being very marked when the plants are grown in concentrated culture solutions of high osmotic pressure.

Somewhat higher in the scale are forms that show polarity, this polarity being already determined in the free swimming spore from which the plant arises. The forward end of the spore attaches itself, and probably in response to the contact stimulus, develops a root-like organ. There is thus a certain degree of specialization shown in the different parts of the plant and this becomes more pronounced in the more highly specialized algæ. While in the simplest forms the cells are nearly alike, in the larger and more complex types there is a greater or less degree of specialization of the tissues and organs more or less directly correlated with the responses to various stimuli. For example, organs resembling the leaves of the higher plants occur in some algæ, these leaf-like structures being evidently organs especially adapted to the work of photosynthesis. There also may be modifications in these large algæ of the tissues associated with protection against loss of water, for conduction, storage, etc., or adaptations enabling the plant to withstand the beating of the surf.

From these humble beginnings have gradually de-

veloped all the myriad forms of plant life that now exist upon the earth.

**Are Ontogenetic Variations Inherited?**—Different individuals of the same species in the course of their development may be subject to very different conditions, and these differences are reflected in the change of form or in structural modifications that are often very marked indeed. That such changes arising in the course of ontogeny may assume hereditary characters has not been positively proved, but it is quite probable that where changed environmental conditions exist for very long periods of time, the ontogenetic structural changes might be fixed, thus assuming hereditary value. Where, for instance, plants from cold countries are grown in milder ones, their habits may be much altered. Trees which are deciduous in cold climates may hold their leaves much longer or even assume an ever-green habit when transferred to a warmer country. The time of flowering is also much influenced by climate. For instance, in the mild, even temperature of the coast region of California, many garden flowers which in the Eastern States have a marked seasonal growth and flower at a definite time, may flower almost at any time of the year, depending mainly upon the amount of water given them, water being the principal factor in plant growth in this region where it is never cold enough to entirely stop growth. Many spring flowering plants, such as the iris, primrose, violets, and many

others often begin to flower in the autumn and continue flowering for several months, and autumn flowering plants like the chrysanthemum may prolong their flowering period until February or March.

How far these changes are intensified by long cultivation in a new environment, has not been critically studied, and of course if the plants were restored to the colder climates from which they came, they would have to revert to their original habits or perish, as their changed habits of growth would be quite impossible in their original habitat.

#### THE CONDITIONS FOR PLANT GROWTH

Of the external factors that govern the life of normal green plants the most important are light, heat, gravity, water, oxygen, and various food constituents, including  $\text{CO}_2$ .

**Light.**—As all green plants are dependent upon light for their existence, it is quite comprehensible that light has evidently exercised a very powerful formative action upon plant structures. The form of each individual plant is markedly influenced by the character of the light to which it is exposed; a fact readily verified by the most casual observation. The bending of plants towards the light, the weak spindling growth where the light is insufficient, and the complete suppression of chlorophyll and the reduction in the size of the leaves, which are such common phenomena where light is excluded,

are familiar to every one. The bleached potato sprouts in a cellar, or the yellow blades of grass under a board, are sufficiently striking examples of the effect of the exclusion of light. As might be expected, the parts most conspicuously affected are those directly associated with photosynthesis. This is seen in the great reduction of the leaf surface and the absence of chlorophyll in most of the higher plants when they are grown in darkness.

**Reaction of Unicellular Plants to Light.**—The modifications of the plant body associated with light adaptation are by no means confined to the higher plants. Unicellular plants often react very promptly to light, moving toward the light when they are motile or shifting the position of their chromatophores according to the direction and intensity of the light rays. A similar shifting of the chromatophores in response to light may be demonstrated also in the cells of the higher plants. The form of the chromatophores also may be explained as a case of light adaptation. They are most commonly flattened discs or thin plates of various forms, thus exposing large surfaces to the light rays.

**Photosynthetic Organs of the Lower Plants.**—Low down in the scale of plant life there is evidence of the development of special structures associated with photosynthesis. Two types of photosynthetic adaptation are met with among the lower algæ. In some of these, like the sea-lettuce (*Ulva*), the whole plant has the form of a thin lamina or thallus, thus

displaying a large surface of green tissue to the action of light; in other algæ there may be dense tufts of small branches whose cells have large chromatophores. In both of these cases there is evidently an increase in the number of green cells

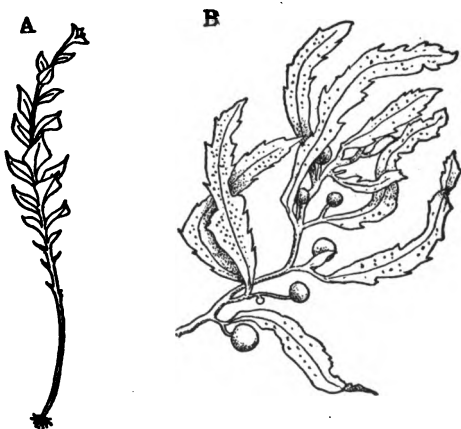


FIG. 2

Development of similar leaf-like photosynthetic organs in two quite unrelated plants.

A—A moss (*Tetraphis*).

B—An alga (*Sargassum*).

with a corresponding increase in the capacity for carbon assimilation.

In some of the highly organized seaweeds, like the kelps, there are definite leaf-like organs attached to the stem or axis of the plant. This differentiation of stem and leaves resembles to a remarkable degree, externally, the corresponding

structures in the highest plants; but it is perfectly clear that the stem and leaves in the seaweed and the seed-plant have no genetic connection, but have arisen quite independently in the course of evolution in the very widely separated plants, in response to the same needs. We meet with the same phenomenon again among the mosses, where there are developed perfect leaves of a type quite different from those of either the seaweed or the flowering plant.

The extraordinary variety of leaf structures found among the flowering plants can usually be correlated with special adaptations to light conditions, and the adaptability of individual plants in this respect is extraordinarily great. A further discussion of the relations of plants to light must be left for another chapter.

**Range of Temperature Suitable for Plant Growth.**

—An indispensable condition for the manifestation of life in any organism is a suitable temperature. However, there may be a great deal of difference shown by different plants in the range of temperatures which they can endure. As a rule all manifestations of life cease in plants when the surrounding medium is cooled to the freezing point of fresh water ( $0^{\circ}$  C.), but some seaweeds thrive in water which may fall below this temperature and seldom has its temperature much above  $0^{\circ}$  C. Such cold water algæ are quickly killed by a temperature only a few degrees above the freezing point, while

other low forms growing in hot springs like those of Yellowstone Park and elsewhere are said to endure a temperature of  $85^{\circ}$  C. or even more. Some bacteria, also, thrive in similar high temperatures which would be immediately fatal to most plants. These heat-loving organisms must have protoplasm of somewhat different constitution from that of most plants, as a temperature much lower than that at which they thrive causes the coagulation of the albuminous contents of the cells of most plants, and this means the death of the protoplasm.

Among the higher plants, many of the desert forms, under the fierce rays of an unclouded tropical sun, must be exposed to temperatures which would quickly destroy the protoplasm of the living cells were these not amply protected so that they are not fully exposed to the untempered heat of the sun's rays. Naturally plants of warm regions differ much from those of colder countries in the range of temperature suitable for their growth. Thus while the common white mustard of Northern Europe will germinate at a temperature near the freezing point, Indian corn, which is of tropical origin, requires  $9^{\circ}$  C. before its seeds will sprout. The optimum temperature for the mustard is  $27^{\circ}$ , the maximum temperature which it will endure being  $37^{\circ}$ . For corn the optimum and maximum temperatures are respectively  $34^{\circ}$  and  $46^{\circ}$ , but the latter figure refers to the endurance of the plant when placed in water

of the given temperature. Where the root is in the soil an air temperature of  $52^{\circ}$  can be borne.

**Modifications Due to Temperature.**—While a suitable temperature is necessary for normal plant growth, the formative effects of different temperatures are far less evident than those due to light. Perhaps the most evident manifestations which seem to be due to temperature are the protective devices seen in plants of cold regions, but these same effects may also be produced by deficiencies of moisture. The deciduous habit and the development of scale-clad winter buds may be cited as examples of such temperature modifications, but very similar effects may be noted in plants living in regions where there is a marked dry season. Under such conditions many trees shed their leaves in much the same way that they do in colder climates. In California, for example, the native buckeye casts its leaves during the long dry summer, and develops resting buds quite like the winter buds of the forest trees of Eastern America.

As an example of the formative effect of temperature among the lower plants can be cited the experiments of Brefeld upon one of the toadstools (*Coprinus*). In this fungus it was found that the umbrella-shaped fruiting body was formed in light at a temperature of  $12^{\circ}$ , but in darkness its development required  $15^{\circ}$ . So also it has been stated that certain fern spores, which at ordinary temperatures will not germinate at all in

darkness, will do so if the temperature is raised to  $32^{\circ}$ . It has also been demonstrated that the character of the nutrition may affect the power of the plant to endure higher temperatures. Thus Theile found that the common blue mold (*Penicillium*) would cease to grow at a temperature of  $31^{\circ}$  when cultivated in a sugar solution, but would endure a temperature of from  $35^{\circ}$  to  $36^{\circ}$  when fed with formic acid and glycerine.

**Endurance of Cold by Seeds.**—There seems to be no degree of cold which is sufficient to kill dormant protoplasm. Perfectly dry seeds of various kinds have been exposed to the temperature of liquid hydrogen ( $-200^{\circ}$ ), without affecting the power of germination later on when exposed to suitable conditions.

**Relation to Water.**—We have already seen that the activity of protoplasm is dependent upon an adequate water supply, and therefore the presence of water is essential for the growth of all plants. The water supply is perhaps the most powerful agency of all in determining the form of the plant and its organs. In its normal condition the cell is strongly distended, and tissues composed of such turgid cells are firm and elastic. With the withdrawal of a portion of the water the tissue becomes flaccid—"wilts," as the gardener says of the plant which droops for lack of sufficient water. To maintain the tissues in their normal turgid condition, the plant must provide for a loss of water due to evapora-

tion, and for this purpose there have been developed in the higher plants special organs, roots, for the absorption of water. There have also arisen extremely efficient tissues for its distribution throughout the plant.

Provision has also to be made for checking excessive loss of water through evaporation. Where plants are completely submerged, whether they are simple seaweeds or more highly developed plants like the pond-weeds, eel grass, etc., there is free communication between the water within the cells and that outside the plant. The specific gravity of the plant is not greatly different from that of the surrounding medium which buoys it up without the need of its developing special supporting tissues, and the seaweed or other submerged plant collapses completely when removed from the water which has served to support it.

**Modification Due to Aquatic Life.**—The difference in habit of the same species grown in water and out of it is strikingly shown in a good many amphibious plants. Thus the common yellow pond lily (*Nuphar*), grown in deep water, has a leaf stalk long and flexible, and the leaves lie flat upon the surface of the water. The same plant growing in shallow water, or, as sometimes occurs, simply on the exposed mud, has short and stout leaf stalks which bear the narrower and firmer leaves completely erect. Another common aquatic plant, the arrow-head (*Sagittaria*), often has two sorts of

leaves; very narrow submersed ones with no blade, and large aërial leaves borne on stout stalks with broad arrow-shaped blade. In various other aquatics, like the water crow-foot, there are submersed leaves which are finely divided, while the aërial leaves are broad. The general tendency in submersed leaves is to assume a very long slender form, or to be divided into many fine segments. These finely divided leaves remind one of the filamentous structure of many algæ, and probably this adaptation is efficient in exposing a larger surface for the absorption of  $\text{CO}_2$  and oxygen in the water, where these substances are less abundant than they are in the atmosphere.

So long as the plants are completely submersed, loss of water by evaporation is impossible; but so soon as they are exposed to the air evaporation is very rapid and the algæ or other aquatic plants wither very quickly when thus exposed. Where, however, algæ are regularly exposed for a certain time, as happens with many of the seaweeds that grow between tide marks, they usually develop gelatinous or mucilaginous substances which retain water with great tenacity, and such algæ may be exposed to the air or even to the hot sun for several hours without losing sufficient water to injure them. When, however, a plant is habitually exposed to the air, as is the case with a typical land plant, all of the exposed surfaces develop a more or less thickened cuticle which is impervious to water.

**Changes Due to Terrestrial Habit.**—The translation to land involves at once a complete readjustment of the plant to its water relation. The exposed surfaces must be protected against excessive evaporation, and this, of course, implies a diminution of the power of absorbing water from without. While some land plants, like certain Californian mosses and ferns, and the resurrection plant (*Selaginella lepidophylla*) of Arizona, can absorb water through their leaves, thus behaving like algæ, this is not possible in most land plants, which procure their water mainly through the root system. The need for rapid distribution of water through the plant is met by the development of an elaborate “fibro-vascular” system of tissue in the higher plants.

The ability of the plant to regulate the loss of water through evaporation may be readily demonstrated by comparing plants of the same species grown under different conditions. Where moisture is abundant and the need of economy small, the rank-growing plant has thick stems and large thin leaves with a poorly developed cuticle. This same plant grown in full sunshine, with a limited water supply, is comparatively small, and not only is there a smaller surface exposed to evaporation, but the surface tissues are very much less permeable. These latter conditions are most pronounced in plants of hot dry regions where the problem of existence is concerned first of all with

the question of water. It is not always easy to distinguish between modifications due to light and those concerned with the water supply. Thin, broad shade leaves are correlated with the necessity of a greater amount of chlorophyll tissue, owing to the less powerful illumination, and also with the lessened evaporation due to the moisture in the air and lower temperature of the deep shade. Many of the lower plants, such as the algæ and mosses which are not able to survive complete drying up, but which must provide against any such contingency, have evolved reproductive cells—spores—which are fitted to resist prolonged desiccation. In the seed-plants there have also been developed special structures—seeds, bulbs, tubers, etc.—which enable these plants to pass unharmed through periods of drought or cold which are fatal to the plant in its active condition. These reproductive structures absorb water promptly and begin to grow when proper conditions are presented.

**Formative Effects of Gravity.**—The continually acting force of gravity undoubtedly exercises a powerful formative effect upon all plant structures, but the nature of this influence is still very obscure. As a rule aërial shoots grow upwards, and are said to be negatively geotropic, while roots growing downward are positively geotropic. A young seedling placed horizontally will quickly show an upward curvature of the shoot and a downward bending of the root. Should the force of gravity be

eliminated by revolving the plant so that all portions are equally exposed to the influence of gravity this curvature will be absent. The many mechanical stresses due to the action of gravity must exercise a pronounced influence upon the growth of all organs exposed to them. For example, the continual pull due to the weight of a leaf or branch must react upon the growing cells of the organs and influence the development of tissues.

**The Necessary Chemical Constituents of Plants.**

—The growth of plants is dependent on the presence of certain chemical elements which are indispensable as food, or are in some way bound up with the constructive processes going on in the plant. The growth of the plant is often very greatly affected by the presence or absence of certain elements which form a very insignificant part of its substance, but which are evidently indispensable in the processes of growth. Thus a plant cultivated in an artificially made nutrient solution containing all the essential chemical elements except potassium or iron, will show very little growth, although the amount of iron or potassium present in the tissues is excessively small; but if entirely deprived of these elements the plant is quickly dwarfed and growth will be almost entirely suspended.

The movements of motile plant cells may be markedly affected by the attractive power of certain substances, and this chemical attraction has been named Chemotaxis. Thus many bacteria will quickly

move towards the source of oxygen, and under a cover glass may be seen to assemble near the edge of the glass where the oxygen is more abundant. They also will quickly gather about green plant cells where oxygen is being given off under the influence of light. Bacteria are also powerfully attracted by certain organic solutions. Chemotaxis plays an important part also in the attraction of the motile male cells, or sperms, to the eggs. It has been shown by Pfeffer, in the case of some of the ferns, that when the archegonium, the organ containing the egg cell, opens, a substance is ejected which contains some combination of malic acid, and this exercises a powerful attraction upon the sperms in response to which they quickly crowd into the open archegonium and thus reach the egg within it. A suitable solution of malic acid placed in a fine glass tube will cause the free sperms to swim into it much as they do into the open archegonium.

The investigations of Klebs have shown that in many of the lower plants the character of the reproductive cells may be largely controlled by the nature of the medium in which the plants are grown. Thus in a low alga, the water net (*Hydrodictyon*), the formation of the non-sexual reproductive cells, zoöspores, may be induced by cultivating the plants in a solution of maltose, while if placed in a solution of cane-sugar, there is an extraordinary development of the sexual reproductive cells. In this connection we may also cite the in-

vestigations of Loeb in artificial parthenogenesis, in which he has shown that certain chemical stimuli may replace to a certain extent the function of the spermatozoa in normal fertilization.

### SELECTION

The last, but not the least, factor to consider is selection. After a variation has appeared, whatever may have been its cause, it remains to be seen whether or not such a variation has sufficient potency to maintain itself. The deciding factor in the persistence and cumulation of any line of variation is Natural Selection, which is the final arbiter in determining what forms shall survive as species or groups of species.

## CHAPTER III

### THE LOWER PLANTS

**I**N endeavoring to trace the pedigree of the vegetable kingdom, we can rely on the record of the past only to a limited extent. While many plants have left perfectly recognizable fossil remains, the record is extremely fragmentary. This is especially true of the delicate and more perishable plants, such as the seaweeds and mosses. Nevertheless most important results have been obtained from the careful study of fossil plant remains.

**Comparative Morphology as a Guide to Relationships.**—On the assumption that all plants are more or less closely related, a comparison of the structures of the living forms affords a clue to the degree of relationship, and hence the great stress which is laid upon the importance of Comparative Morphology. In view, however, of the ready response of plant structures to changes in environment, great caution must be exercised in distinguishing true homologies from similarities in structure due to response to similar conditions. We have already pointed out, for instance, that leaf-like organs have developed in plants of widely separate origin, e.g., seaweeds, mosses, and the higher land plants. These

leaves are in no sense homologous organs and do not point to any close relationship between the plants which possess them. A proper study of comparative morphology must take into account all the organs of the forms compared, but it also is evident that some of these organs are much more important in heredity than others. It is also necessary to distinguish between structures which are readily affected by external conditions and those which show evidence of being more permanent in character. The reproductive parts are as a rule much more stable than the vegetative organs, and are rightly considered to hold the first place in indicating affinities between plants. For example, the vegetative organs, especially the leaves, are rudimentary in such a plant as the Indian pipe (*Monotropa*), which has entirely lost the power of the photosynthesis and feeds on organic substances. The flower, however, is but little altered, and shows its unmistakable relationship to the rhododendron, huckleberry, and other heath-like plants.

**Embryology.**—The study of the development of the plant and of its different organs, or embryology, in its wider sense, is of great importance. Here also great care must be taken in determining what are primitive characters and what are merely adaptations. Of late, much attention has been given to Experimental Morphology, or the critical study of the direct effects of various stimuli upon the developing organism. While there is good reason to suppose that much valuable information as to the

factors governing the development of plants is to be obtained from such experimental work, the problems are so exceedingly complicated that great caution must be exercised in drawing general conclusions. Our ignorance of so many of the conditions that have governed the evolution of any plant in the past, and the long time that may elapse before the reactions resulting from a stimulus show themselves, emphasize the necessity for extreme caution in making sweeping generalizations from the results of any experiments. Nevertheless such work is exceedingly valuable in checking and extending the results derived from other sources, such as paleontology and comparative morphology.

There still exist organisms that may very well be not very different from the first living things that appeared upon the earth. These are the Bacteria, those ubiquitous "germs," cells so minute that under the most powerful microscope many of them appear merely as tiny specks too small to show any definite structure.

These minute organisms, however, are of the highest importance in the economy of nature, as it is to their activity that most forms of organic decomposition are due, and this decomposition is essential in order that inorganic compounds may be reduced to simpler ones that are available as food for the higher plants. In the earth there are myriads of other bacteria whose activity results in the fixing of the atmospheric nitrogen, and the produc-

tion of nitrogenous compounds suitable for plant food.

**Blue-green Algæ.**—Probably related to some of the bacteria are certain common plants of low organization, called, from their color, the blue-green algæ (Cyanophyceæ), and these, with the bacteria, constitute a group of plants known as the Schizophyta, or fission plants, as their only form of propagation is by means of simple cell division. Some of these blue-green algæ occur as slimy, blackish green films on wet earth or on objects in the water, while others give rise to jelly-like masses, often of considerable size, in which the plants are imbedded. Some of these organisms occur in hot springs like those in the Yellowstone Park, and like many of the bacteria they are able to endure temperatures which are fatal to most plants. Like the bacteria, also, the blue-green algæ show a very primitive cell structure, and are presumably very ancient types, but it is by no means certain that either these forms or the bacteria are related directly to the higher plants.

**Flagellata.**—Many bacteria are actively motile, being provided with cilia so that they resemble somewhat the low organisms known as the Flagellata. The Flagellata are also presumably very primitive organisms. In the structure of their cells they resemble the lower types of plants and animals, and there is some reason to suppose that they more closely resemble the progenitors of both the higher

plants and animals than do any other existing organisms. The flagellates were long looked upon as a division of the Infusoria, the most important group of unicellular animals, but recent studies on these forms have shown that there are two well-marked types, one of which possesses the chromatophores or chlorophyll-corpuscles characteristic of

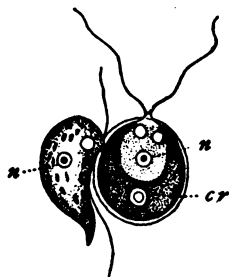


FIG. 3

A colorless flagellate, *Bodo caudatus*, attacking a flagellate unicellular plant, *Chlamydomonas*, which possesses a green chromatophore, *cr*. A nucleus, *n*, is present in each organism. (After Bütschli.)

the typical plants, while in the others the chromatophores are wanting. All flagellates possess cilia or flagella, by means of which they are propelled through the water. The green flagellates closely resemble many of the lower green plants, which often give rise to free swimming reproductive cells very closely resembling these flagellates and suggesting that the latter are related to the ancestors of the higher green algæ. On the other hand, the

colorless flagellates show a close structural resemblance to the cells of such low animal types as the simple sponges, and the derivation of these animals from flagellate ancestors is readily conceivable. The flagellates may thus be said to represent an extremely ancient structural type from which have been developed, on the one hand colorless animal forms, and on the other green plants.

The pigment-bearing flagellates show a tendency to approach the non-motile condition of the typical plants. This tendency toward the immobile condition may perhaps be correlated with the presence of chlorophyll and the resulting ability to assimilate inorganic food. The colorless flagellates, not having this property, would require greater power of movement in their search for food; i.e., their nutrition is typically animal. With the establishment of these two great lines of development—plants and animals—the characteristics of each become more pronounced, and above the flagellates any organism may be easily referred either to the animal or vegetable kingdom.

**Volvocales.**—In studying the various forms of life that abound in fresh-water ponds, we often find, actively swimming about, certain green cells which may be solitary, or which may be united in globular bodies large enough to be seen with the naked eye. The best known of these organisms is *Volvox*, whose globular body may contain thousands of cells and is easily seen. Most of these

"Volvocales" are composed of a much smaller number of cells, and some of them are unicellular (see Fig. 3). Under certain conditions, the cell divisions take place with great rapidity and within a few days a small pool or watering trough may have its waters made quite green by the presence of millions of these little plants.

The structure of the cells in *Volvox* is like that of most of the lower green plants. Each cell has a single large green chromatophore. There is a distinct nucleus and there is also a peculiar body, red in color, and apparently an organ for light perception, hence often known as the eye spot. These organisms are extremely sensitive to light, and by means of the two cilia with which each cell is provided they swim toward the source of light. This moving toward the light is undoubtedly associated with the function of photosynthesis.

New plants arise by division of special cells, and as we have seen, these divisions may follow very rapidly, so that the number of individuals may increase enormously in a very short time. Another form of reproduction, however, occurs at the end of the growing season, at which time there are developed special structures fitted to survive the drying up of the water, which is fatal to the plant in its active condition. These structures are the "resting spores," which are provided with a thick cell wall and contain an accumulation of food materials, so that they are thus protected against the effects

of drought, and the food supply within the cells permits of very rapid germination when the proper time comes. These "resting spores" are the result of a simple sexual process. Two special cells, the "gametes" or sexual cells, fuse into a single one, and the resulting cell, or "zygote," becomes the resting spore. In the unicellular forms, the gametes are alike, both being provided with cilia and hardly distinguishable from the ordinary individuals; but in the higher forms, like *Volvox*, one of the gametes is a very small and active cell, the male or sperm cell, while the other is very much larger and is destitute of cilia. The latter is the female cell—egg, or ovum—and when fertilized by the sperm, develops into the resting spore.

Because of their permanently motile condition, and their unmistakable resemblance to the Flagellata, the *Volvocales* are sometimes claimed by zoölogists as animals; but the cell structure and the reproduction are in all respects like those of the lower algæ, and there is no question but that the relationship with the latter is a very close one.

Among the unicellular *Volvocales* it is not uncommon to find the plants assuming a quiescent condition. The cilia are lost, and the cell then closely resembles many of the ordinary unicellular algæ. It is highly probable that the lower green algæ originated in some such fashion from unicellular *Volvocales*, this being indicated by the frequent reversion in so many algæ to the motile condition

in the form of zoöspores, which are identical in structure with the cells of Volvox.

**Multicellular Algæ.**—While a good many of the lower algæ remain unicellular, more of them are multicellular organisms. Among the simplest of these multicellular algæ are the various “pond-scums,” those soft, foamy green masses so often seen floating on stagnant water. These plants consist of chains of entirely similar cells floating free in the water. Others of these low algæ, such as the one shown in Fig. 4, B, are attached, and the basal cell may develop root-like outgrowths so as to form a definite organ of attachment. These plants often multiply by means of zoöspores, little, naked, free-swimming cells closely resembling the cells of Volvox. After a short period of activity, these zoöspores settle down, develop a cell wall, and thus for a short period assume a typically unicellular condition. By repeated divisions, this cell then gives rise to the characteristic filament, or cell row. It will be seen, then, that in its development the plant passes successively through the free, motile stage, and the stationary unicellular condition, before it finally attains its adult multicellular state.

**Photosynthetic Organs in Algæ.**—From these simple beginnings there may be traced many intermediate stages leading up to the branched or broad flattened bodies which distinguish the more complicated types of algæ. This increase in the complex-

ity of the plant body is usually associated with the increase in the amount of green tissue. The most important function of the plant's life, aside from

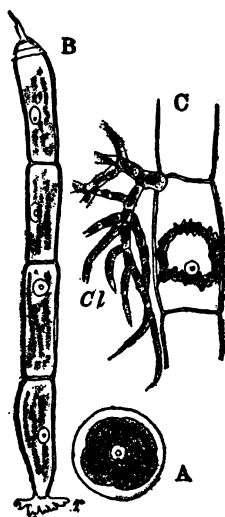


FIG. 4

Evolution of the plant body in the lower green plants.

A—Unicellular plant (Pleurococcus).

B—Unbranched filament, with basal root-like organ, or hold fast (*r*) (Ædogonium).

C—A confervoid alga, Draparnaldia, in which there is a photosynthetic apparatus consisting of tufts of densely crowded green cells, *Cl*.

reproduction, is the process of photosynthesis; hence the adjustment of the green cells to the light exposure is of prime importance, and this adjustment explains some of the most striking modifications of

the primitive plant body. In such forms as that shown in Fig. 4, C, the chlorophyll is mainly restricted to small cells, whose number is increased by the extensive branching of the filaments, so that there arise dense tufts of small green cells, which might very well be compared to a finely divided leaf, and like the leaf, these may be fairly described as special photosynthetic organs. The flat, leaf-like body of the common sea-lettuce (*Ulva*) and many other algæ illustrate adaptation by which the amount of green tissue exposed to the light is increased.

**Green Algæ; Chlorophyceæ.**—The primitive fresh-water algæ are none of them of very great size, and for the most part they retain a simple structure. Their color is usually a vivid green, unobscured by the red and brown pigments which distinguish most of the large seaweeds. These pure green forms are therefore known as the “Green Algæ,” or Chlorophyceæ. While most of these are confined to fresh water, some of them have migrated to the sea, and in the altered environment have undergone more or less marked changes. The most striking of these green seaweeds are those known as the Siphoneæ, an assemblage of very peculiar green plants distinguished by an almost complete suppression of cell division, so that the plants are composed of a system of open, often very much twisted and branched tubes, without any division walls. A few of these curious plants occur in the cooler seas, but to observe them in their fullest development one

must visit the warm seas of the Tropics, where, especially about the coral reefs, these interesting plants abound. Some of them are fan-shaped, flattened bodies; others jointed, much branched, coral-like plants, sometimes having the ends of the branches tipped with bright green tufts of hairs looking like the tentacles of some polyp. Still others have creeping stems from which arise fern-like leaves and send down into the coral sand fine, branching roots. These plants might almost be called plant-corals, since, like the true corals, they possess a calcareous skeleton and play a more or less important part in building up the coral reefs where they grow. Like the animal corals, also, they have been found abundantly in a fossil condition, and there is some evidence that they already existed in the ancient Silurian seas. For a long time these remains were supposed to be those of animals, and it is only of late that the real nature of these fossil Siphonæ has been recognized.

**Green Algæ Mostly Fresh-water Types.**—With the exception of the Siphonæ, most of which are marine plants, the majority of the green algæ are fresh-water types. There are, however, two great divisions or classes of algæ which constitute the bulk of the marine vegetation, at least along the shore. These are the Brown Algæ, or Phæophyceæ, and the Red Algæ, or Rhodophyceæ, both of which reach greater dimensions than any of the green algæ, and are much more specialized. These are

the seaweeds *par excellence*. Of these two groups the Phæophyceæ are almost exclusively marine, while the red algæ have a number of fresh-water representatives.

**The Brown Algæ.**—Very different from the small and delicate green algæ are the great coarse brown kelps so common along the rocky coasts of the cooler seas. The rocks of the northern New England shore exposed by the tide, are covered with a thick drapery of the common rock-weed, or bladder kelp, and in the deeper water are groves of the big *Laminarias*, “devil’s aprons” in the vernacular. With these are many species, some delicate little plants, but more of them stout and leathery in texture, and all distinguished from the green algæ by the presence of brown or yellow pigments which give them their characteristic olive or leathery brown color. Much the same types occur on the western European coasts, but it is in the Pacific that these remarkable plants reach their greatest development. The visitor to the Pacific Coast, from Alaska to Middle California, is at once struck by the extraordinary variety and gigantic size of some of the common kelps, which attain a length hardly rivaled by any land plants, and make these great seaweeds the giants of their class.

**Giant Kelps.**—Compared with these giants of the Pacific, the largest of the Atlantic kelps are mere pigmies. Two of the Pacific kelps, *Nereocystis* and *Macrocystis*, especially merit the popular name of

**Giant Kelps.** The former is a most striking seaweed of the Northern Pacific Coast, where it is said to reach a length of one hundred meters. Its slender stem is firmly anchored in deep water, reaching to the surface, where it expands a cluster of broad leaves two or three meters in length, and buoyed up by a great bladder-like float as big as a croquet ball. *Macrocystis* is said to reach even a greater length than *Nereocystis*, and great beds of this kelp occur off the California Coast. These beds of kelp, as for instance at Santa Barbara, form very efficient breakwaters.

Some of the kelps, like the curious sea-palm (*Postelsia*) (Fig. 20), are specially adapted to growth in the heaviest surf, and seek the most exposed rocks, where they are subjected to the full force of the great Pacific rollers.

**Gulf Weed.**—Other striking types of the brown algæ are the floating forms like the gulf-weed (*Sargassum*) of the Caribbean Sea, which is drifted northward by the Gulf Stream and is familiar enough to transatlantic voyagers. Many similar forms occur in the warmer seas, and they are especially abundant off the coast of Japan. It is still not settled whether all of these floating species begin life as attached plants, and are subsequently torn from their moorings. That they live for a very long time in the floating condition is shown by the long distances from land at which they occur, in a vigorously growing condition. Some-

times these little floating islands are veritable zoölogical gardens, as a great variety of small marine animals, sometimes including fish, seek shelter among the fronds of the kelp.

The brown algæ are preëminently marine plants. Very rarely do they invade fresh water, and then only in the immediate vicinity of the sea. A large number of them are plants living between tide marks, and they show very perfect adaptation to this condition. Their leathery, gelatinous fronds retain the water very tenaciously, and they may be exposed to the air for a long time without injury. Indeed in the far northern regions like Alaska, where as a rule the air is cool and moist, they often grow so near the high tide mark as to be out of the water for the greater part of the time. It is supposed that the brown pigment with which they are provided is a protection against too great illumination when they are uncovered by the receding tide.

These large brown algæ sometimes show a marked degree of specialization. The massive, tough, and leathery plants often develop structures resembling the stem, root, and leaves of the higher plants. As they very often grow where they are exposed to the full force of the ocean surf, they are provided with powerful root-like organs or hold-fasts, by which they cling tenaciously to the rocks. Thin flat leaf-like organs are of common occurrence, and in connection with these there may be floats, or air vesicles, which buoy up the leaves and keep

them near the surface of the water, where they may have proper exposure to the light. In these great plants there is also internal differentiation shown, especially in the occurrence of elongated elements, which recall the conducting tissues of the higher plants, and presumably serve the same purpose.

There is no reason to suppose that the similarities, either of external form or internal structure, point to any near relationship between the brown seaweeds and any land plants. These resemblances, however, illustrate in a most striking way the formation, in two widely separate groups of organisms, of very similar structures in response to similar needs. It is, in short, a case of "analogy" comparable to the formation of functionally similar, and structurally different, organs in animals; as, for instance, the wings of birds and insects.

**Reproduction of Brown Algæ.**—Some of the brown algæ are purely asexual in their reproduction, while others, like the rock-weed (*Fucus*), have perfectly developed sexual cells. A remarkable fact is that the forms which are the largest, and structurally the most complete, i.e., the giant kelps, are, so far as is known, propagated mainly by non-sexual zoöspores.

**Brown Algæ Probably Not Related to the Green Algæ.**—The origin of the brown algæ is by no means certain. At present the available evidence seems to indicate that they are not directly related to any of the green algæ, but constitute a quite inde-

pendent developmental line, derived from some free-swimming type, perhaps allied to the Flagellata. The zoöspores or asexual reproductive cells of these plants differ from those of the green algæ in having cilia laterally inserted and, of course, possessing a brown pigment. Among the lower alga-like forms are certain types known as Peridineæ, the simpler forms of which are not unlike the zoöspores of the brown algæ, having like them two laterally placed cilia, and it is possible that the beginning of the line which culminates in the great kelps and rock-weeds is to be found in forms resembling the simpler Peridineæ, which in turn are presumably allied to the flagellates.

Another group which is sometimes associated with the flagellates is that of the Diatoms, which offer a large and widely distributed assemblage of unicellular plants, occurring everywhere, both in fresh and salt water. These diatoms, together with the Peridineæ, are the most important constituents of the floating vegetation of the sea, or the "plankton" upon which the animal life of the ocean very largely depends. If any relationship really exists between the diatoms and the higher Phæophyceæ it must be extremely remote, the diatoms themselves giving some evidence that they are a highly specialized group of comparatively recent origin.

**The Red Algæ.**—The very characteristic red algæ, while they comprise a majority of the sea-

weeds, are far less conspicuous than the great kelps, owing both to their much smaller size, and to their growing, as a rule, in deeper water, or under the shelter of larger seaweeds and rocks, where they are easily overlooked. They include some of the most exquisite of all plants, and their beautiful tints and graceful forms are familiar to every one who has made even a casual study of marine plants.

The rose-red pigment which quite hides the green chlorophyll in the living plant is easily extracted by fresh water, and then the presence of chlorophyll is plainly seen. This red pigment probably supplements the chlorophyll in the process of photosynthesis, and enables the chlorophyll bodies to absorb certain light rays which would otherwise be unavailable owing to the deep water in which they grow.

A marked peculiarity of the red seaweeds is the complete absence of any motile reproductive cells, such as are so common in the green and brown algæ. The result of fertilization is not a single spore which directly or indirectly produces a new plant, but there is formed a multicellular structure, or "spore fruit," which by budding gives rise to many spores. The complete absence of any motile cells in the red algæ is difficult to explain, as it is hard to see what advantage this can be to the plant.

The red algæ are not so exclusively marine as the brown seaweeds, and there are a good many species which live in fresh water. These fresh-water forms have, as a rule, but little of the red

pigment, and in both color and structure show a certain resemblance to some of the green algæ with which they may be, perhaps, remotely related.

Whatever may have been their origin, the red algæ, as they now exist, are very highly specialized plants with no evident relation to any higher plant types, and their peculiarities, including the characteristic red pigment, which gives them their name, are presumably adaptations to their marine environment.

**Reproduction in Algæ.**—The algæ exhibit great diversity in their reproduction, which may be sexual or asexual. Several forms of budding or simple fission of the plant body are common and in a few forms it is the only reproduction known.

Thus in all unicellular species, and in many of the lower multicellular forms, the individual plant breaks up into two or more portions, each of which becomes at once a new individual. Very often special reproductive cells are formed, which are able to develop without fertilization into new plants. The commonest of these non-sexual reproductive cells are the zoöspores. In the formation of these zoöspores the protoplasm escapes from a cell, either in a single mass or after a preliminary division into two or more parts, and these on escaping into the water are seen to be provided with cilia by which they swim rapidly about before they settle down and grow into new plants. In their motile condition the zoöspores so closely resemble the low organisms known as Flagellata, and those

curious free-swimming algæ, the Volvocales, that they might readily be mistaken for them.

This frequent reversion to the free-swimming condition, resembling in all respects the fully devel-

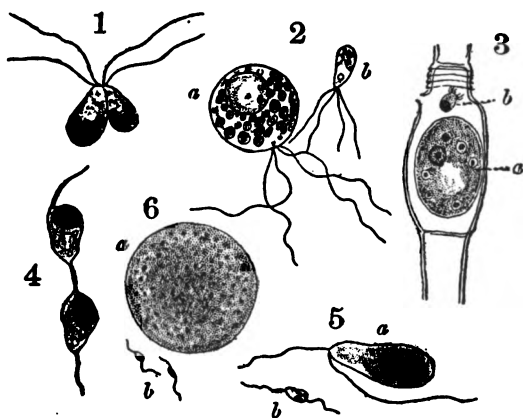


FIG. 5

Evolution of the sexual reproduction in the algæ, showing parallel development in the green and brown algæ. Upper figures, Chlorophyceæ; lower figures, Phæophyceæ; *a*, female gamete; *b*, male gamete.

1, *Pandorina*; 2, *Aphanochæte*; 3, *Ædogonium*; 4, *Ectocarpus*; 5, *Cutleria*; 6, *Fucus*.

Figs. 1-5, after Oltmanns.

oped cells of the lower organisms, is one of the strongest reasons for assuming that the green algæ, at least, are derived from flagellate ancestors.

**Evolution of Sex in Algæ.**—Among the algæ are found a number of groups in which are exhib-

ited in a most instructive fashion the gradual evolution of the sexual reproductive cells. It is clear from a study of these that this evolution has arisen quite independently in several widely separate lines, but the course of evolution is extraordinarily similar in all of these. The Volvocales and the Ulothricales, among the green algæ, are excellent examples of this, and the brown algæ also show all stages of evolution of the gametes or sexual cells, from perfectly similar ones, hardly distinguishable from the non-sexual zoöspores, to clearly differentiated small male cells or spermatozoids and large non-motile female cells or eggs (Fig. 5).

The difference between the lowest type of sexual cells and the non-sexual zoöspores is very slight, and there seems no question that the gametes were originally derived from cells capable of development without fertilization. Fertilization in its simplest form consists in the union of two complete and perfectly similar cells, the union extending to the fusion of the nuclei into one, and also possibly the fusion of the chromatophores. In the course of development the two gametes become more and more dissimilar, one diminishing in size but usually remaining actively motile, the other becoming larger and losing the power of motion. The first is the male gamete or sperm, and is largely composed of the nucleus of the mother cell; the large, passive cell is the female cell, egg, or ovum. Among the lower types the gametes may sometimes germinate

without union, thus showing but little difference from the non-sexual zoöspores. Cases are known also, even among some of the more specialized forms, where the egg will develop into a new plant without fertilization.

**Asexual Algæ.**—Some highly developed algæ are, apparently, entirely destitute of any sexual reproduction. Until recently it was supposed that the giant kelps reproduced themselves by non-sexual zoöspores only, but it has been found that the supposed zoöspores are sometimes, at least, gametes. So also the curious siphonous alga *Caulerpa*, so far as is now known, multiplies only by the separation of a portion of the plant.

In the fresh-water green algæ the fertilized egg usually develops into a thick-walled "spore" or zygote. This is capable of enduring long periods of drought and is presumably a provision for carrying the plant through unfavorable conditions, especially drought or cold. These resting spores almost never are formed in marine plants, as the latter never are subject to prolonged periods of desiccation. The zygote on germination very often gives rise to a number of zoöspores, by a division of its protoplasm, and thus a new generation starts at once with several individuals.

In the red seaweeds there is a marked difference in the results of fertilization from that found in the green or brown algæ. Instead of the female cell developing at once into a resting spore, it is at once

stimulated into active growth and gives rise either directly or indirectly to a peculiar structure known as the "Sporocarp," from which the spores are ultimately developed. The development of the sporocarp is too elaborate to be given here in detail, but the resulting structure may be compared in a way to the spore-bearing structure or "sporophyte," which arises from the fertilized egg in the mosses or ferns, although there is not the least evidence of any relationship between the latter forms and the red algæ. In both groups, however, the product of fertilization is a spore-bearing structure, which to a greater or less degree is parasitic upon the plant which bears the sexual organs, and there is a more or less well-marked "alternation of generations."

**Summary: The Fresh-water Algæ More Primitive than the Seaweeds.**—A survey of the Algæ as a whole indicates that the main line of development in the direction of the higher plants is through the green algæ, which give evidence of being a much more primitive group than either the brown or red algæ. There is a fairly complete series of forms leading from the free-swimming Volvocales, through non-motile unicellular forms, to simple filamentous or thallose green algæ, which in their turn lead toward the lowest of the land plants, the simpler mosses. From this main line there probably diverged several secondary developmental lines such as the Siphonææ and Charales. The two other classes, the brown and

red algæ, are forms which have become most perfectly adapted to strictly marine life, most of the more primitive green algæ being confined to fresh water. Of the two classes of seaweeds the brown algæ probably constitute a separate line, derived from some flagellate ancestors. The red algæ, while different in many ways from the green algæ, still among their lower members show points of resemblance which do not forbid the hypothesis that they may have arisen from forms allied to some of the green algæ. This view is strengthened by the fact that a good many of the more primitive types of the red algæ inhabit fresh water. The true brown algæ are almost exclusively marine in habit.

If, as has been conjectured, the ancient seas were much less saline than those of the present time, it may be that the green algæ as they now exist are the little changed descendants of the primordial algal types which have persisted in fresh water and retained most of their original characteristics. The brown algæ, so far as we can judge, are essentially marine, and both color and structure may be considered to be direct adaptations to the marine life. The brown pigment is assumed to be protective, as these plants are often exposed to strong light when uncovered by the tides, and the leathery texture and gelatinous tissues of the larger forms are evidently associated with their growth on exposed rocky shores.

## THE FUNGI

The algæ are the plants which may be considered to show the most perfect adaptation to aquatic life, the aquatic ferns and seed plants being probably the descendants of terrestrial forms which have reverted to the aquatic habit. There are, however, certain plants of somewhat heterogeneous nature which differ very widely in their habits from the normal plants and have become extraordinarily modified so that it is practically impossible to trace their ancestry. These are the Fungi, which include such familiar forms as mushrooms, molds, mildews, rusts, an enormous assemblage of species, second in number only to the flowering plants. The Fungi never possess chlorophyll, and so far as is known are quite unable to assimilate  $\text{CO}_2$  for food, and hence they are dependent upon organic matter for their carbon, just as animals are; but some of them, like the nitrogen bacteria, can use the atmospheric nitrogen.

A bit of bread exposed to moist warm air soon becomes covered with a growth of mold, which an examination will show to include a number of quite different species. These arise from tiny spores which germinate upon the moist bread and quickly produce a tangled, webby mass of fine threads which ramify through the bread, breaking down the starch by means of the ferments or enzymes secreted by the invading fungus filaments, and using the starch for food. Similarly, a mushroom growing in a

meadow manured by the animals feeding upon the grass, sends its filaments deep into the rich earth, where they form extensive white root-like fibers which attack the organic matter in the soil much as the mold attacks the starch in the bread. The conspicuous, umbrella-shaped mushroom is merely the fructification of the plant, most of whose existence is passed under ground. Such fungi as the molds and toadstools, which live upon dead matter, are known as saprophytes.

Quite different in their habits are the parasitic fungi, which attack living animals and plants, and are the causes of many of the most serious plant diseases. A common animal parasite is the little fungus that often kills house flies in the autumn, and causes the infected insect to stick to a window-pane, where it is surrounded by a halo of tiny spores shot off from the ends of the filaments that protrude from the body of the fly, within which the fungus has finally completed its work of destruction.

A familiar vegetable parasite is the mildew which so often appears upon rose leaves, distorting them and covering the diseased area with a gray frost-like film. In this case the parasite lives upon the surface of the host-plant, and simply sends little suckers into the cells, and thus obtains the necessary food. Other parasitic fungi, like the rusts, live within the body of the host-plant, and break through the surface only for the purpose of distributing their spores.

An examination of the cells of a fungus shows

that there is no trace of the chromatophores that give the green color to most plants. The fungi are therefore unable to perform photosynthesis, and so far as we know, must obtain their carbon from the organized carbon compounds of other plants or animals.

**Origin of Fungi.**—It is generally assumed that the fungi are descended from plants containing chlorophyll, although this is not universally admitted, and it is conceivable that the true fungi represent a series of forms which have never possessed chlorophyll. A comparatively small number of fungi, usually associated under the name of Alga-fungi, show a more or less evident resemblance to certain algæ, and some of them at least may very safely be considered to be of algal origin. It is an open question, however, whether these alga-fungi are really related at all to the true fungi, or, indeed, whether they all are related among themselves. There is some reason to suppose that some at least of the true fungi are really derived from these alga-fungi; but this point is by no means certain.

Among the most alga-like of the fungi are the water molds (Fig. 6), whose resemblance to certain algæ, both in structure of the plant and its reproduction, is sufficiently close to make probable a real relationship between the forms. The water molds are found growing upon the bodies of dead insects or other animals in the water, and sometimes are parasitic, attacking young fish or older ones that have been wounded. The slender,

more or less branched tubular filaments have no division walls, and, except for the absence of chlorophyll, resemble very closely a common green alga, *Vaucheria*. As in the latter, there are two sorts of

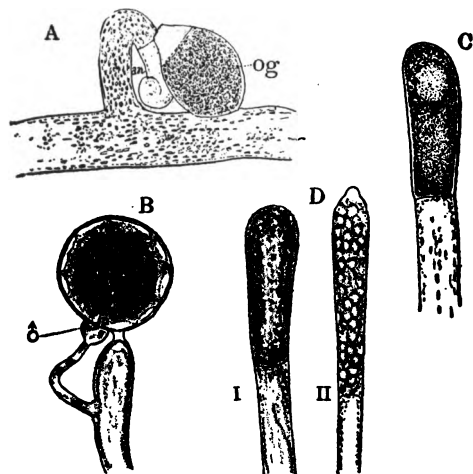


FIG. 6

- A—Sexual reproductive organs of a siphonous alga, *Vaucheria*, compared with those of a water-mold, *Rhipididium*, B.  
 C—Zoösporangium of *Vaucheria*.  
 D—Zoösporangium of a water-mold, *Saprolegnia*.  
 B—After Thaxter.

reproductive organs, non-sexual zoöspores, and sexually produced resting spores.

**Eumycetes or True Fungi.**—The 40,000 or more species known as true fungi, or Eumycetes, present an almost hopeless tangle of forms which is just beginning to be unraveled. At present the classifica-

tion is in a very chaotic condition, although much is being done to clear up some of the most puzzling questions relating to their development and affinities. We may for convenience's sake divide them into two classes, Ascomycetes, or Sac-fungi, and Basidiomycetes, which include the familiar mushrooms, puff-balls, etc. It must be confessed, however, that only with difficulty can a good many forms be brought within these categories; and as to the relation of these two groups to each other and to the alga-fungi there is much difference of opinion.

**Sac-fungi, Ascomycetes.**—Among the simpler sac-fungi are many species known popularly as mildews, which are often troublesome parasites upon various plants. The common rose-mildew (*Sphærotheca*) is one of the best known. Another closely related species, which has been carefully studied, is common on the dandelion. The body of the fungus, or "mycelium" as it is technically called, consists of a mass of slender filaments composed of rows of long cells, which form a film over the surface of the leaf on which it is growing. Into the epidermal cells of the leaf are sent little suckers by means of which the fungus feeds, and presently it sends up upright branches into the air, from which little spores are cut off in rapid succession and quickly grow into a new mycelium if the conditions are favorable.

Another type of spore is produced also by most of the mildews. As the result of a simple form of sexual reproduction, two cells unite and the con-

tents of one passes into the other and fuses with it. The fertilized cell is stimulated into growth and produces finally one or more sac-shaped cells, the "asci" or spore sacs, within which are produced usually eight spores. All of the typical sac-fungi develop sooner or later spores of this type, from which the class receives its name. The spore sacs are only occasionally exposed, as for instance in the fungus *Exoascus*, which causes the disease of peach trees known as "leaf curl." Usually there is developed a protective envelope of sterile tissue so that the spore sacs are contained in a definite fruiting body or "sporocarp," which may reach considerable dimensions as in the scarlet cup-fungi which are sometimes encountered in damp woods.

While the development of this spore fruit may be preceded by the fertilization of a definite "ascogonium," in most of the large forms like the cup-fungi this has not been demonstrated, and a true fertilization is probably wanting.

**Basidiomycetes.**—The mushrooms, toadstools, puff-balls, and rusts represent the second great division, or class of the true fungi, the Basidiomycetes. In the large forms, such as the mushroom, the spore fruits arise from the extensively developed mycelium in the earth or rotten wood upon which the fungus is growing. The spore fruits are often of large size and characteristic form, and upon certain portions are borne the spores. In the mushroom they arise from the surface of the "gills," the

pendent radiating plates upon the lower side of the cap. The spores are borne upon swollen club-shaped cells, or basidia, and each spore is attached to a short, slender stalk from which it is readily detached.

In the lower types of Basidiomycetes, such as the wheat-rust, the spore fruits are much less definite in form, and several different sorts of spores are produced in the course of the plant's development.

Nuclear fusions occur at certain times, and these fusions, in some of the lower Basidiomycetes, perhaps represent a very rudimentary type of fertilization. The relation of the Basidiomycetes to the sac-fungi is not at all clear, and it is not unlikely that the two classes are not related at all.

**Nutrition of Fungi.**—The fungi, as we have seen, differ very essentially in their nutrition from the green plants, being unable, so far as we know, to utilize inorganic matter, except in the case of nitrogen, for the manufacture of organic food. Much remains to be learned, however, about the nutrition, which is often extremely peculiar. Many fungi feed upon dead substances and are therefore important agents in organic decomposition. Others are parasites, and often show extraordinary specialization. A very remarkable type of parasitism is that known as "heterœcism," where the parasite lives on more than one host. This is the case in many rusts, one of the commonest cases in Eastern America being that of the rust *Gymnosporangium*, which produces the conspicuous galls known as "cedar apples"

upon species of Juniper. Upon these cedar apples in the spring are produced great masses of orange-yellow spores imbedded in a soft jelly. From these spores arise others which will not grow upon the cedar, but will germinate if they are carried to the opening leaves of a thorn or crab apple, upon which they produce a fungus growth entirely different in appearance from that upon the cedar. In little cup-shaped receptacles which appear later upon the leaves of the thorn, are borne chains of spores, which, carried back to the cedar, give rise to a new crop of cedar apples. What is the meaning of this change of host is not clear, but it is paralleled by the behavior of many animal parasites like *Trichina* and the liver-flukes.

**Symbiosis.**—Many fungi live in a more or less perfect symbiotic relation with other plants. The best-known cases are those of the Lichens, which, as is well known to the botanist, are associations of fungi, usually sac-fungi, with various low algæ. If we examine the structure of a lichen, it is easy to see that it is much like a true fungus, but enmeshed among the colorless filaments of the fungus are colonies of green cells, which a close examination shows to be unicellular algæ, upon which the fungus filaments are parasitic. It is these green cells, imprisoned in the tangle of fungus filaments, which give the greenish tinge to the lichen. Exactly what rôle each of the symbionts plays is not entirely clear. The fungus is undoubtedly to some

extent parasitic upon the alga and cannot exist without it. On the other hand, the alga can, and not infrequently does, grow quite independent of the fungus. However, it is by no means unlikely that the latter furnishes to the alga certain food constituents, probably including nitrogen. Moreover, the fungus conserves water in such a way that the alga cells associated with it are able to grow as they could not do if they were exposed to the air.

A good many flowering plants, especially those which are deficient in chlorophyll and especially those that grow in humus like the Indian-pipe and certain orchids, have associated with them a fungus which in some way, not very clearly understood, furnishes them with certain food constituents from the humus in which the plants are growing and make them available for the use of the plants. Recent studies on these forms have shown that sometimes the fungi possess the power of fixing free nitrogen, like the nitrogen bacteria, and it is likely that the associated symbiont gets the benefit of this by its association with the fungus, as well as obtaining the carbon which it cannot fix for itself by photosynthesis. Some ferns and liverworts also show this symbiotic association with fungi.

Many species of parasitic fungi must be of comparatively recent origin, as they are restricted to a single host, which in many cases is a highly specialized flowering plant and must be a relatively recent development.

## CHAPTER IV

### THE ORIGIN OF LAND PLANTS

**T**HE algæ seem to have reached their culmination in such great marine forms as the giant kelps of the Pacific. These highly specialized brown seaweeds and the very peculiar red algæ are the dominant plants of the ocean at the present time, and have evidently best solved the problem of life in salt water; to their peculiar environment are no doubt due their most marked characteristics. There is little reason to suppose that any higher plant types have arisen from either the brown or the red algæ, although it has been surmised that there may be a possible connection between the latter and certain fungi.

#### **Green Algæ the Ancestors of the Land Plants.—**

The green algæ, on the other hand, probably represent the remnants of the primordial vegetation which have persisted in fresh water without any very great alteration down to the present time. It is from forms allied to these primitive green algæ that there is good reason to suppose the first land plants arose.

Except for differences in temperature, conditions

of life in fresh water are very uniform everywhere, and it is not strange therefore that the range of structure exhibited by the fresh-water green algæ is comparatively slight. Owing to the density of the medium in which they live, no mechanical or supporting tissues are required, as they are entirely supported by the water. In consequence most algæ when taken from the water collapse. Moreover, owing to their complete submersion there is no loss of water from evaporation, and the cells, therefore, are not protected against evaporation and water is absorbed by all of the superficial cells.

**Fresh-water Plants Require Protection Against Desiccation.**—However, as most fresh-water plants are liable to be destroyed by the drying up of the temporary ponds or streams in which they live, it is necessary to provide for their survival through periods of drought to which they may be subjected. Marine plants never being exposed to prolonged drying up, although they may be uncovered by low tide for several hours, have no need for such protective devices, and hence, resting spores are rarely found in these marine forms. Some of the lowest plants, like certain of the blue-green algæ and the common “*Protococcus*” forms, may be completely dried up in their vegetative condition, remaining dormant for an indefinite period, and then when water is supplied to them promptly revive and resume their activity. Moreover, some of these low forms, as well as others of higher rank, find suf-

ficient moisture for their needs upon the surface of the shaded ground or the sheltered sides of tree trunks and walls. They readily absorb water from the moist substratum or from the air, and this is sufficient for their normal growth. A small number of algæ, e.g., *Botrydium* (Fig. 7), regularly

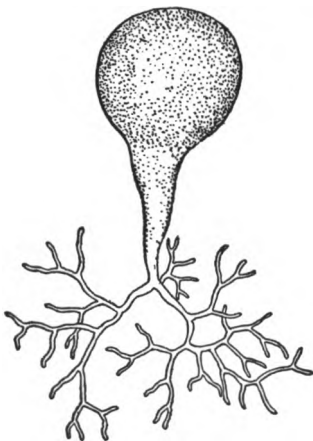


FIG. 7

*Botrydium*, a terrestrial alga provided with roots for taking up water. Much enlarged.

grow entirely exposed to the air and obtain their water from the earth by means of root-like organs, thus behaving like genuine land plants; but owing to their extreme delicacy the period of growth is usually very brief, and as their cells are not adequately protected against loss of water by evaporation, they can only reach very small dimensions.

**Resting Spores of Green Algæ.**—Most of the green algæ at the close of their active growing period produce some form of resting spore, thick-walled cells which can survive complete desiccation, and are thus able to carry the plant over periods of drought. While a small number of algæ, like the *Botrydium* already referred to, may assume a more or less complete aërial habit, this is exceptional, and we must look to the next branch, or sub-kingdom, of plants, comprising the mosses and ferns, for the first green plants which may be considered to be normally of terrestrial habit.

**The First Terrestrial Plants.**—The first invasion of the land by the algal ancestors of the higher plants must be regarded as a most momentous event in the history of the vegetable kingdom. The much greater range of conditions on land affords far greater possibilities for structural variation, and this is amply shown in the future history of the plant kingdom. The higher plants are mainly organisms adapted to life in the air, and show a complexity and variety of structure far surpassing that of the largest and most specialized of the seaweeds, which seem to have attained the limits of structure possible within the range of their strictly aquatic environment. The mosses and ferns, as we shall see, show unmistakable evidence of their derivation from aquatic ancestors, and indeed all of these forms may be considered to be amphibious, as the development of certain phases

of their life history is dependent upon the presence of free water.

**Modifications Due to Terrestrial Habit.**—When the plant exchanges its aquatic environment for life on land it must undergo some radical changes in structure. First of all is the necessity for economizing water, as it is no longer able to take in water at all points, and it must therefore provide both for the absorption of water and for checking undue loss of water through transpiration. Hence have arisen the special water-absorbing roots, and the protection of all the exposed cell walls by a cuticle or impervious membrane, which materially checks the escape of water through evaporation.

The lowest of these land plants, such as the liverworts and mosses, are often prostrate in their habit and do not assume the upright position common to most of the higher plants. This prostrate habit, which implies an imperfect development of mechanical or supporting tissues, recalls the behavior of their algal ancestors. Where the upright position is assumed, it involves a greater or less development of firm tissues, the so-called mechanical or supporting tissues, which give to the plant sufficient rigidity to overcome the force of gravity. With the increasing size of the plant comes the need for rapid transportation of water, and there have arisen in response to this need the characteristic conducting tissues, which reach their highest development in

the so-called "vascular" plants, the ferns and flowering plants.

**The First Land Plants Allied to Liverworts.**—Certain liverworts probably resemble pretty closely the first land plants. These are small plants of very simple structure, lying flat upon the ground, to which they are attached by delicate roots. Structurally these liverworts are some of them less complex than many of the algæ, often being composed of almost perfectly uniform cells. They show

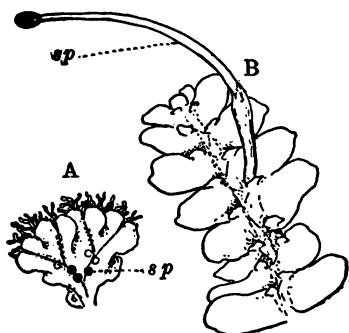


FIG. 8

A—A simple liverwort, *Ricciocarpus*, showing the small globular sporophytes, *sp*, imbedded in the thallus.

B—A large liverwort, *Treubia*, having leaf-like organs; the sporophyte has a long stalk or seta, carrying up the terminal spore-bearing capsule.

certain resemblances to some of the simple algæ, especially the order known as the Ulothricales, which on the whole come nearer to the liverworts than do any other algæ. It must be admitted, how-

ever, that the gap between the algæ and the mosses is a very wide one.

Occasionally liverworts are found which are true water plants, such, for example, as *Ricciocarpus* (Fig. 8, A), which grows ordinarily as a floating aquatic. If the water dries up, however, the liverwort settles upon the mud and grows very luxuriantly, the contact with the earth acting apparently as a stimulus. Roots are developed penetrating the mud and the plant assumes quite a different form from that of the floating condition. The behavior of this liverwort may perhaps illustrate the first step in the development of the higher plants from alga-like aquatic ancestors. These water plants stranded upon the mud by the subsidence of the water may have developed roots in response to contact stimulus of the solid earth, and prolonged their growing period, and thus may have inaugurated the line of land plants which was destined to become the dominant plant type of the future.

**Amphibious Nature of the Archegoniates.**—The essentially amphibious nature of the mosses and ferns is best shown in their method of fertilization. If we examine a liverwort like that shown in the figure, we shall find the sexual cells, eggs, and sperms borne in organs of characteristic structure. The female organ (Fig. 9, C) is multicellular and usually has the form of a long-necked flask, which contains the egg-cell. This structure is called the archegonium and is remarkably uniform in struc-

ture in all mosses and ferns, which are hence called the "Archegoniates." The male organ, or antheridium, is also multicellular and contains many sperm cells, each of which gives rise to a ciliate

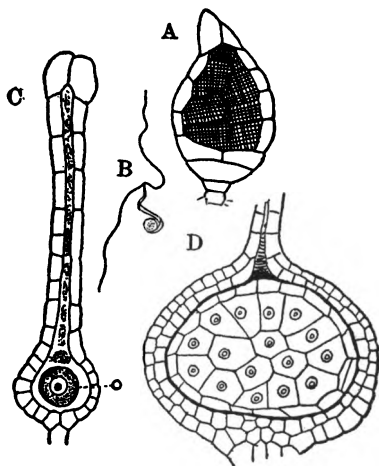


FIG. 9

A—Section of the antheridium or male organ of a liverwort, *Riccia*.

B—The motile male gamete, or sperm.

C—The female organ, or archegonium, containing the female gamete, or egg, *o*.

D—The embryo-sporophyte enclosed in the enlarged basal part of the archegonium.

sperm much like that of certain algæ (Fig. 9, A, B). Neither archegonium nor antheridium will open unless wet; but if the ripe organs are covered with water they will promptly open, and the liberated sperms then swim to the open archegonium,

which they enter, and one of them fertilizes the egg in precisely the same way as happens in the permanently aquatic algæ.

After the egg is fertilized it becomes invested with a cell-wall, but it does not enter a resting state as is the case with the green algæ. Instead of this, the egg cell grows and undergoes repeated cell-divisions, so that a cellular body, the embryo, results (Fig. 9, D). The embryo, by further growth, finally develops into a plant which is entirely different in appearance from the one which bears the archegonium, and which is called the gametophyte or sexual plant. The plant developed from the embryo does not become independent, but remains attached to the sexual plant, upon which it lives in a parasitic fashion. Sooner or later it gives rise to special reproductive cells, which are produced by cell-division and are hence non-sexual in their nature. These are called "spores," and the plant bearing them is known as the "sporophyte," or non-sexual plant.

**Alternation of Generations.**—The sporophyte assumes greater and greater importance in the course of the evolution of the archegoniates, while the gametophyte becomes less and less conspicuous. From the spores produced by the sporophyte there arise new gametophytes. This alternation of the sexual plant or gametophyte with the neutral one, or sporophyte, produced as the result of fertilization, constitutes the frequently discussed "alternation

of generations" which characterizes all of the higher plants.

## **Evolution of the Gametophyte in Bryophytes.—**

The gametophyte in the simpler liverworts is not strikingly different from some of the algæ, and, as we have seen, may be a delicate prostrate thallus, composed of almost uniform cells except for hair-like roots or rhizoids, and the reproductive organs. From this simple type of gametophyte there may be traced several diverging structural types. The gametophyte reaches its highest degree of specialization in some of the larger mosses where there are developed leafy shoots of considerable size, a foot or more in length occasionally, and these show a specialization of the tissues which may be almost compared to that of the sporophyte of the ferns. The roots, however, never assume the perfect form found in the ferns and seed-plants, but are usually composed of a single cell. The mosses often depend only to a limited extent upon these hair-like roots to supply them with water, absorbing the water readily through the leaves very much as the algæ do. Liverworts and mosses together form the group of Bryophytes.

The apparent inability of the gametophyte to develop adequate roots, probably accounts for its failure to reach dimensions at all comparable to those of the sporophyte of the higher plants. Moreover, none of the large gametophytic structures have developed a mechanical system of tissues sufficient

to enable them to maintain a truly upright position. The larger species are either prostrate, as we have seen in many large liverworts, or the upright position is maintained by the shoots being densely crowded and thus affording mutual support. It must be remembered that the gametophyte of the archegoniates is the transformed progeny of some strictly aquatic plant, and it is not unlikely that there are limits beyond which such a type cannot progress. So far as we know, the higher mosses represent the extreme development on land of these originally aquatic organisms, and they cannot be said to have solved very satisfactorily the problem of the development of a plant type perfectly adapted to life on the land.

**Evolution of the Sporophyte.**—The further evolution of the plant kingdom is mainly bound up with the neutral generation or sporophyte. The origin of this is to be looked for in the zygote, or resting spore, so commonly developed in the green algæ, as the last phase of their life history. This zygote may be said to represent the terrestrial phase of the alga, as it is fitted to survive drought, and thus to carry the plant over from one growing period to another. The fact that the zygote, which is the morphological equivalent of the sporophyte of the mosses and ferns, is from the very first a structure fitted for existence outside the water, must be borne in mind in following out the further history of the evolution of the higher plants.

In those algæ which are assumed to be the nearest relatives of the archegoniates, the zygote on germination produces by division of its contents several spores which in most cases are motile zoöspores. This division of the zygote's contents into several spores, each of which produces a new plant, gives of course an advantage over those forms in which the zygote develops at once into a single plant. In one of these green algæ, *Coleochæte*, there is a material growth in the size of the egg after it has been fertilized, and when the spore germinates there is developed a comparatively large multicellular body which resembles the embryo-sporophyte formed in the liverwort, and is the nearest approach to this structure that has yet been discovered among the algæ. Whether or not this resemblance indicates a true relationship has been much discussed and is still not satisfactorily settled. It is pretty evident, however, that the sporophyte of the first archegoniates must have been derived from some structure which could not have been very different from the sporophyte of *Coleochæte*.

A study of the evolution of the sporophyte in the lower existing archegoniates demonstrates clearly the course of development leading up to the higher plant types. In *Riccia*, for example, the globular mass of tissue derived from the growth and division of the egg has practically all of its cells devoted to spore formation, there being only a single layer of sterile tissue upon the outside (Fig. 10, A).

Each of the inner cells divides into the four spores, a constant character in all archegoniates. These spores are usually capable of resisting drought, and correspond physiologically to the single zygote of the algæ. The retention of the embryo sporophyte within the archegonium, and its nourishment at the expense of the gametophyte, enable it to prolong its period of growth, with a corresponding ability to increase its output of spores—a great advantage to the plant, as a single fertilization thus results in a very much increased number of spores as compared with the simpler algæ.

Even in the simplest sporophyte, like that of *Riccia*, a small amount of tissue remains sterile, i.e., does not give rise to spores. In all the other types the amount of sterile tissue is very much increased, and it soon begins to develop into special structures, indicative of a division of labor, and this involves a much longer growing period for the developing sporophyte. In most liverworts (Fig. 10, B) the lower part of the embryo is very early separated from the upper portion from which the spores are developed, and this lower part becomes a definite organ of absorption, the foot, by means of which food is taken from the tissues of the gametophyte for the nutrition of the embryo-sporophyte, which thus may be said to live parasitically upon the parent gametophyte. Other structures may also develop from the sterile tissue, such as the elongated seta or stalk, which may reach a con-

siderable length, and facilitates the disposal of the spores developed in the upper region of the sporophyte (Fig. 8, B). The latter forms a capsule en-

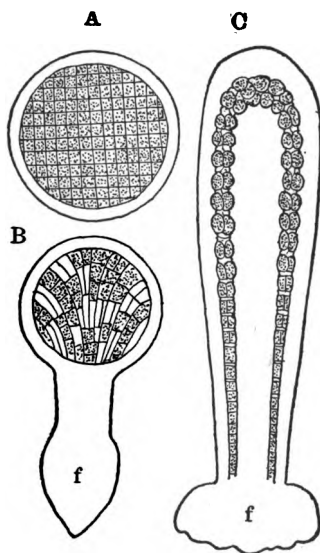


FIG. 10

Diagrams illustrating the evolution of the sporophyte in the liverworts. The shaded areas show the extent of the sporogenous tissue; f, the foot.

A—Riccia.

B—Porella.

C—Anthoceros.

closing the spores, together with peculiar sterile cells, or elaters, formed from a portion of the potentially sporogenous tissue.

**Subordination of Spore Production in the Higher Archegoniates.**—Among the liverworts proper, the function of the sporophyte is almost entirely spore production, and it develops little or no chlorophyll, so that it is capable of very little independent growth. In two other classes of the bryophytes, viz., the true mosses and the horned liverworts (*Anthocerotes*), the sporophyte becomes much more important and spore production is to a considerable extent subordinated to the vegetative life of the sporophyte. In these forms the growing period of the sporophyte may last for several months before the spores are finally developed, and only a relatively small portion of the sporophytic tissue gives rise to spores (Fig. 10, C). A large amount of green tissue is present in the outer portion of the sporophyte, and this may form a spongy green tissue quite like that in the leaves of the higher plants. As in the latter, this green assimilative tissue may communicate with the atmosphere by means of special pores or stomata, which structurally closely resemble those of the vascular plants. By means of these well developed chlorophyll-bearing tissues, the sporophyte can assimilate the  $\text{CO}_2$  of the atmosphere, and it is quite independent of the gametophyte for its supply of organic food. In some of the true mosses the green tissue is largely segregated at the base of a capsule, where it forms a sort of assimilative organ known as the apophysis. This may be said to take the place, physiologically at least, of a leaf. There

are also present in many of the true mosses, extremely specialized structures associated with the opening of the sporogonium and the scattering of the spores. These very highly differentiated structures indicate that the true mosses constitute a very specialized class with little direct affinity with any other plants. They may be said to bear somewhat the same relation to the relatively primitive liverworts that red and brown seaweeds do to the more primitive green algæ.

**Anthocerotes.**—There is one family of liverworts, now usually considered to represent a distinct class, which is especially important in the study of the evolution of the sporophyte. These are the horned liverworts (Anthocerotes), which in the character of their sporophyte approach more nearly the condition found in the ferns than is the case with any other bryophyte. The gametophyte of these Anthocerotes is very simple in structure, and in the character of the cell which contains only a single chloroplast they resemble the green algæ more nearly than do any other liverworts.

**Sporophyte of Anthoceros.**—It is the sporophyte, however, with which we are here especially concerned. In its most highly developed form, i.e., Anthoceros (Fig. 10, C), it shows a remarkable power of growth. There is developed a basal zone of growing tissue, which keeps adding to the size of the sporophyte so that sometimes it may reach the length of ten centimeters or more. To support this

long-continued growth, a very large bulbous foot is developed, and, although this has no direct connection with the earth, there may sometimes be seen to be an extraordinary development of roots from the under side of the gametophyte immediately below it, and this unusual development of the roots is obviously induced by the protracted growth of the sporophyte, and its increased need for a greater supply of water. The large sporophyte becomes almost independent of the gametophyte, but not wholly so, as it is still dependent upon it for its supply of water. The upper part of the sporophyte shows a well-developed epidermis, perforated by numerous stomata, exactly like those of the higher plants. Beneath the epidermis are several layers of green cells with intercellular spaces communicating with the openings of the stomata, and this green tissue, both in structure and function, closely resembles the mesophyll or green tissue of an ordinary leaf.

The axis of the sporophyte is occupied by a strand of much elongated cells, which are presumably more or less active agents in the conduction of water, and possibly may be regarded as the equivalent of the vascular bundle, which occupies a similar position in the young organs of the sporophyte in the so-called "vascular" plants. In *Anthoceros*, the spore-producing tissue is reduced to a single layer of cells situated below the green assimilative tissue. There is sometimes a more or less complete separation of this tissue into fertile and sterile areas,

the former being enclosed in the meshes of a net-like complex of sterile cells. This segregation of the sporogenous cells into groups is probably the first hint of the definite spore-bearing organs or sporangia, which are characteristic of the ferns. Were the sporophyte of *Anthoceros* to develop a true root, i.e., to come into direct contact with the source of water supply and soil constituents, the sporophyte would be rendered quite independent, since the highly developed photosynthetic apparatus is ample to provide for the assimilation of  $\text{CO}_2$ .

Whether or not the *Anthocerot*es are considered to be directly related to the ancestors of the Pteridophytes, or ferns, there is no question that both in the character of the reproductive organs and that of the sporophyte, they resemble more nearly the Pteridophytes than do any other liverworts.

**Sporophyte First Becomes Independent in the Ferns.**—Although in *Anthoceros* and the higher mosses, the sporophyte attains a large measure of independence, it never becomes entirely independent of the gametophyte upon which it must draw for its water supply, owing to the failure to make direct connection with the earth. In the second division of the Archegoniates, on the other hand, the Pteridophytes or Ferns, the young sporophyte at an early period develops a true root (Fig. 11, A, *r*), which pierces the tissues of the gametophyte and grows downward into the ground, so that the young sporophyte henceforward absorbs its water supply

directly from the earth, and the sporophyte for the first time assumes the form of an entirely independent plant. For a greater or less time, however, it remains attached to the gametophyte and develops

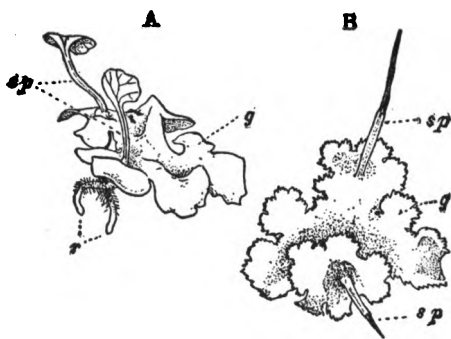


FIG. 11

A—Gametophyte, *g*, of a fern, *Danæa*, bearing two young sporophytes, *sp*. Each sporophyte has produced a leaf above and a root, *r*, below.

B—Gametophyte of a liverwort, *Megaceros*, with two sporophytes; the latter, unlike those of the fern, have no root.

a foot very similar in structure and function to that found in the sporophyte of the bryophytes.

**The Gametophyte of the Fern.**—If the spores of a fern are sown upon moist earth, there will presently be developed a little green thallus, the gametophyte (Fig. 11, A, *g*), which does not in the least resemble a fern, but in appearance is very much like some of the simpler liverworts, and has its nearest analogue perhaps in the horned liverworts, whose reproductive organs, both antheridium and arche-

gonium, show some interesting resemblances in structure to those of the lower ferns. The archegonium and antheridium in all their essential features are very similar to those in the liverworts and mosses, and, as in those, water is essential both for the opening of the ripe reproductive organs and for the conveyance of the motile sperms. Its dependence upon water and the presence of these motile sperms clearly indicate the aquatic origin of the gametophyte.

There is much difference among the different groups of pteridophytes in the degree of the development of the gametophyte and as might be expected, those forms which for other reasons may be assumed to be the oldest and most primitive types, are those in which the gametophyte is most important and most nearly resembles that of the hypothetical liverwort-like progenitors. In some of the more primitive ferns (Fig. 11, A), the gametophyte may reach an inch or so in length and may live for several years, not always dying after the sporophyte has become established. In some of the more specialized ferns, on the other hand, like the so-called water ferns, the whole life of the gametophyte may extend over less than twenty-four hours.

In their fertilization and early development of the embryo-sporophyte, the ferns closely resemble the simpler liverworts, but sooner or later there is evident the development of special organs,

which are absent from the embryo of the liverworts. There is soon formed an outgrowth which breaks through the overlying tissues of the gametophyte and expands itself in the light as a little fan-shaped green leaf. Another outgrowth pushes downward and penetrates the soil and forms the primary root, while a third structure becomes the permanent growing point, or stem apex of the little sporophyte, which is now recognizable as the young fern (Fig. 11, A). During its early development, the little sporophyte draws its nourishment from the gametophyte by means of a foot quite like that found in the mosses and liverworts, but so soon as the first leaf is expanded, and the primary root has penetrated the earth, the young sporophyte becomes an independent plant.

In the ferns the development of spores is often delayed for many years, the sporophyte in the meantime increasing in size and developing special organs and tissues which characterize these "vascular" plants. The young sporophyte soon shows a definite axis or stem, which usually possesses a permanent growing point, from which arise later on many leaves and roots. An extensive system of conducting tissue is a characteristic of the sporophyte of the ferns, which are called sometimes for this reason "vascular cryptogams." This "fibro-vascular" system constitutes a tissue especially modified for water conduction and for the transport of food substances. While similar tissues, as we have seen, may

be found in some of the large algæ, like the great kelps, and also in various mosses, they never reach the perfect development that distinguishes them in the sporophytes of the ferns and seed-plants.

**The Root of Pteridophytes.**—With the development of the primary root, which, unlike the hair-like “rhizoids” of the gametophyte, is a massive structure capable of extensive growth and admirably fitted for the absorption of the water from the soil and its transportation to the different organs of the sporophyte, the independence of the sporophyte is for the first time perfectly established; and we have henceforth to deal with plants which are not modifications of an originally aquatic type, as is the case with the gametophyte, but are elaborations of a structure, the zygote or resting spore of the algæ, which is from the beginning a structure adapted to terrestrial conditions. This probably accounts for the perfect adaptation of the sporophyte to terrestrial life, when compared with the indifferent success as land plants of even the most perfect gametophytic structures, like those of the larger mosses. The latter, owing to their failure to develop an adequate root system, seem to have about exhausted the possibilities of the aquatic gametophyte, and the further development of the vegetable kingdom is mainly bound up with the amplification of the terrestrial sporophyte. With the inauguration of this entirely new plant type begins the most important chapter in the history of the vegetable kingdom.

### The Sporophyte of the Fern a Long-lived Plant.

—The sporophyte of the fern, unlike that of the

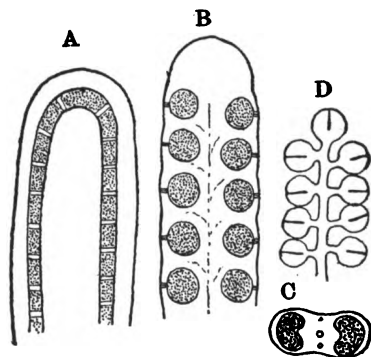


FIG. 12

Diagrams to show the possible method of evolution of the sporangia of the lower ferns.

A—Section of the upper part of the sporophyte of *Anthoceros*, a liverwort in which the sporogenous tissue is imperfectly divided into fertile areas by the intervention of sterile cells; these are unshaded in the diagram.

B—Section of the sporangiophore of a very simple fern, *Ophioglossum*. The originally continuous sporogenous tissue becomes divided into distinct masses of fertile tissue, separated by wide partitions of sterile tissue; each sporangium opens separately.

C—Cross-section of B.

D—Sporangia of *Botrychium*, a fern closely related to *Ophioglossum*, but having much better differentiated sporangia, each opening by a transverse slit.

mosses and liverworts, is not limited in its growth, and its life does not end with the dispersal of the ripe spores. It may even live for many years and

attain very imposing dimensions, some of the tree-ferns rivaling the palms in size and beauty. The original stem apex often persists, but new leaves and roots are produced to meet the needs of the developing sporophyte, which may live for a century or more. Sooner or later spores are produced, the development following very close that noted for the liverworts and mosses; but in the ferns the spores are borne in special organs or sporangia, which in the simpler types like the adder-tongue ferns (Fig. 12, B, C) suggest somewhat the condition found in *Anthoceros*.

The curious horsetails or scouring rushes common in low ground and moist thickets represent a second class of pteridophytes which differ strikingly in their habits from the ferns. The hollow-jointed stems with the leaves reduced to toothed sheaths encircling the joints, together with the characteristic cones which bear the spore cases, at once distinguish the horsetails from the other pteridophytes (Fig. 13, C, D). The elongated, pendent sacs, or sporangia, containing the spores, are arranged about the margins of the umbrella-shaped "sporangioophores" which make up the terminal cones. In their structure and development the sporangia are not essentially different from those of the lower ferns.

About twenty-five species, all belonging to the genus *Equisetum*, are all that are known to exist at the present day, the insignificant remnant of the many large and complex horsetails that flourished in

earlier geological times. Unlike the ferns as these plants are in their general habit, they nevertheless show many points of resemblance to the lower ferns in their characters, both of gametophyte and sporophyte, and it is probable that there is a real, although remote relationship existing between the horsetails and ferns.

In the Northern forests one often finds covering the ground, evergreen trailing plants whose slender creeping stems send up little branching shoots closely set with small leaves, so that they suggest little evergreen trees. These are "club-mosses" belonging to the genus *Lycopodium*, and one of them, popularly known as "ground-pine," is every year sent in great quantities to the Northern markets at Christmas time for making wreaths and festoons. These club-mosses, or Lycopods, represent a third class of pteridophytes, which differ so much from the ferns and horsetails as to make it likely that they are not at all related to them, but have originated quite independently (Fig. 13, A).

A second genus, *Selaginella*, contains several hundred species, a few of which occur in temperate regions, but most of them are tropical. A number of species are common in greenhouses, where their delicate moss-like foliage is very ornamental. These cultivated species are often erroneously called *Lycopodium*, but may be distinguished from the true *Lycopodiums* by having two sorts of spores, large and small. In the character of its spores,

Selaginella comes nearer the seed-bearing plants than does any other living pteridophyte.

**Paleozoic Pteridophytes.**—The horsetails and club-mosses were once very much better developed

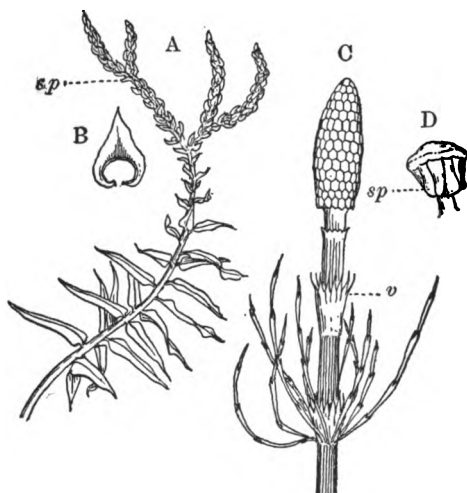


FIG. 13

A—A club-moss, *Lycopodium*, showing the spore-bearing cone, or strobilus, *sp*.

B—A sporophyll with its single sporangium.

C—A horsetail, *Equisetum*, showing the sheath-like leaves, *v*, and the terminal cone made up of the sporangiophores, a single one of which is shown in D—*sp*, sporangia.

than at the present time, this being especially the case in the Paleozoic types. Many of the Paleozoic pteridophytes reached tree-like dimensions and showed a secondary growth in thickness of their stems comparable to that which is found in most

living trees. This secondary thickening occurs in a slight degree in a few living ferns, and it is clear that this peculiar development has arisen quite independently in all of the main groups of pteridophytes, but has been lost in most of the descendants of the Paleozoic pteridophytes. In the club-mosses there are developed minute sperms with two cilia like those of the mosses, while in the ferns and horsetails the sperms are very much larger and have numerous cilia, and do not at all resemble the sperms of any known bryophyte.

While in the lower types of the pteridophytes, like some species of *Lycopodium* and the lower ferns, the gametophyte may reach a size comparable with that of many liverworts, in the more specialized types there is a great reduction in the size of the gametophyte which may live a very short time.

A peculiar modification of the gametophyte is sometimes met with. This is the development of a subterranean habit, with the entire loss of chlorophyll. The gametophyte thus becomes saprophytic, living upon the leaf mold or the soil rich in organic matter. To enable it to do this it has associated itself with a fungus, much like that found in the subterranean organs of certain saprophytic flowering plants. In some way, not perfectly understood, it is through the agency of this "endophyte" supplied with carbon and perhaps also with nitrogenous matter.

**Heterospory.**—In the horsetails, and in certain ferns, the gametophyte is unisexual, the male plants being usually smaller than the female, which of course has to support the young sporophyte. This separation of the sexes is the first step in the direction of what is known as “heterospory,” i.e., the production of two sorts of spores, large and small, developing respectively female and male gametophytes. The large spores are known as macrospores or megaspores, the small ones, microspores. In all cases of heterospory, the gametophytes are much reduced in size, this being especially true of the males, which may consist of a few cells only, and have their whole development completed within less than twenty-four hours. The most marked case of this is shown in the water fern, *Marsilia*. In this plant only one spore comes to maturity in the megasporangium, while in the microsporangium all of the spores mature. If the ripe spores are placed in water of a suitable temperature, growth begins at once, and in a common Californian species, within from fifteen to twenty hours the gametophytes are completely developed and fertilization has been effected. The spermatozoid fertilizes the archegonium, and from the egg the young sporophyte, which closely resembles that of the typical ferns, is quickly developed.

Heterospory has arisen in several quite unrelated groups of Pteridophytes, and it is clear from a study of the fossil forms that a number of the hetero-

sporous types which once existed are now quite extinct. This tendency towards heterospory in so many unrelated groups is an interesting case of parallel development, and may be compared to the separate evolution of sexual cells in widely separate groups of algæ, or the development of a similar fibro-vascular system in such probably unrelated types as the ferns and club-mosses. There are four quite distinct existing families of heterosporous pteridophytes, two of which show unmistakable evidence of being derived from two types of "homosporous" ferns. One of the others is unmistakably related to the club-mosses; the second is of somewhat doubtful affinity.

The evolution of heterospory in so many unrelated groups of pteridophytes is of importance in connection with the question of the origin of seeds, the structures which especially distinguish the highest plant types. The separation of the male and female gametophytes, and the reduction of these, are the first steps in the evolution of the seed. In all of the existing pteridophytes, except the genus *Salvinella*, the germination of the spore and the development of the gametophyte takes place after the spores are shed, although it may be said that in some of the water-ferns the spores do not become free from the sporangium, which is detached with the spores inside it. In some of the water ferns the reduction of the female gametophyte is less than in the other heterosporous forms and chlorophyll

is developed, so that the gametophyte is to some extent self-supporting, while in other forms the growth is either entirely at the expense of material stored up in the spore, or in *Selaginella*, as we shall presently see, the gametophyte is nourished directly from the tissues of the sporophyte, thus reversing the relation of sporophyte to gametophyte as compared with the lower archegoniates.

In *Selaginella* germination takes place in the megaspore while it is still in the sporangium, and long before it has reached its full size. At this time the spore contains but little protoplasm, and the subsequent growth of the gametophyte, which until it is nearly fully grown is included entirely in the spore, is mainly at the expense of the sporophyte. The cells of the sporangium walls remain active, and through them material is drawn from the sporophyte for the nourishment of the developing gametophyte inside the growing spore. The gametophyte may be said, therefore, to grow parasitically upon the sporophyte, thus reversing the conditions which obtain in the lower archegoniates, where it is the sporophyte which derives its nourishment from the tissue of the large green gametophyte in which it is enclosed. The long retention of the germinating spore within the sporangium of *Selaginella* is a further step in the direction of seed formation.

**The Origin of Seeds.**—Much light has been thrown upon the history of the seed-plants by the extensive studies of the Paleozoic fossils, which

have been made within recent years. It is now evident that many fossil plants, formerly supposed to be true ferns, are really seed-bearing plants of a very primitive kind; and it is practically certain that these primitive seed plants have originated more than once from quite distinct types of ferns. It is clearly proved that two of the lowest types of existing seed plants, the Cycads and the curious Ginkgo, or maiden-hair tree, are related to the ferns. Some of the fossil club-mosses, e.g., *Lepidocarpon*, were also seed-bearing plants, and there are some pretty strong reasons to believe that these, or forms not unlike them, may have been the progenitors of another characteristic group of existing seed-plants, the Conifers.

While a few of the Paleozoic horsetails were certainly heterosporous, heterospory was less perfectly developed in this group, and as yet there is no evidence of any seed-bearing plants that can be considered to be allied to the horsetails, and it is probable that this phylum never advanced beyond the heterosporous phase.

**The Nature of the Seed.**—The seed is a further elaboration of the megasporangium. In the seed-plants the latter generally remains attached to the sporophyte until the spore, which is permanently retained within, has completed its development and fertilization has been effected. The embryo-plant, enveloped in the double covering of the spore membrane and the wall of the sporangium, is very ef-

fectively protected from external vicissitudes, and, moreover, during its development can draw upon the parent plant for an unlimited supply of food. It moreover is able to store up in the ripe seed the reserve food necessary for its growth during the early stages of germination. The advance of the resting stage of the plant, from the simple spore in the fern to the embryo within the seed of the seed-plants, gives the latter a great advantage in the certainty and rapidity with which the new generation can be established.

It is positively known that the development of seeds has taken place quite independently in several groups of pteridophytes, and this makes it likely that all of the existing seed-plants are not necessarily descended from a single stock. There is no question of the origin of the cycads and Ginkgo from ferns of some kind, but the evidence of the origin of the other seed-plants from the same source is not so convincing. It has recently been argued by Professor Seward that *Araucaria*, one of the conifers, shows strong evidence of a relation with the tree-like club-mosses of the Coal Measures, and there is much to be said in favor of the derivation of the conifers from quite different forms from those which give rise to the cycads. All of the so-called Gymnosperms, i.e., conifers, cycads, etc., show unmistakable evidences of having originated from some pteridophytic ancestors, but the origin of the higher type of seed-plants, the

Angiosperms or ordinary flowering plants, is the subject of much controversy.

**Alternation of Generations.**—The origin of the pteridophytes is a matter of some difference of opinion. The weight of evidence in favor of the derivation of the leafy sporophyte of these plants from the sporogonium of some form allied to the existing bryophytes is very strong. The greater elaboration of the sporogonium in such forms as the higher mosses and *Anthoceros*, with the increasing subordination of the sporogenous function, shows an unmistakable tendency towards the independence of the sporophyte such as is finally reached by the ferns. Between the latter and the mosses are marked similarities in the character of the tissues, e.g., the development of stomata, the green assimilative tissue of the assimilative organ of the sporophyte, and finally the close correspondence in the details of spore division. These, together with marked similarities in the structure of the gametophyte and the reproductive organs, make it exceedingly probable that the alternation of generations in the pteridophytes is “antithetic,” as it is in the bryophytes; that is, the sporophyte, or neutral generation, is the result of an elaboration of the strictly terrestrial phase of the plant’s life, the lineal descendant of the unicellular zygote or resting spore of some green alga, developed by these humble water plants for enduring periods of drought.

A good many cases of “Apogamy,” or the origin

of the sporophyte as a vegetative bud upon the gametophyte, have been recorded for various ferns, and it has also been found that the gametophyte may develop directly from portions of the sporophyte other than the spores. These phenomena have led to the theory that there is no essential difference between the two generations, and that the sporophyte is not to be considered as homologous with the sporogonium of the bryophytes, but as the direct modification of some gametophytic structure.

The writer has pointed out more than once that these phenomena, which are often pathological, may be very properly compared with numerous cases of adventive budding or regeneration common to so many of the higher plants. Of course there is an essential structural similarity in the cells of the gametophyte and sporophyte, each of which is normally derived from special cells of the other, egg or spore respectively. It is not surprising then that under special conditions, in view of the great power of regeneration exhibited by most plant tissues, that the phenomena of apogamy and apospory should occur. No more remarkable than the production of the whole plant from the root of a poplar, or from a fragment of the leaf of a begonia, where it has not been claimed that the bud is in one case homologous with the root and in the other with the leaf.

**Antiquity of the Pteridophytes.**—It is clear, from the study of Paleozoic fossils, that all the existing

classes of pteridophytes are of great antiquity, and little light is shed upon the origin of these types by the study of the fossil records, as the bryophytic forms from which the pteridophytes are presumably descended have left very few recognizable traces, and we are forced to fall back upon the study of the living forms for clues to their origin. Of the living pteridophytes several types have been assumed to represent the nearest approach to the bryophytic type of sporophyte, and of these there is most evidence in favor of two—*Ophioglossum* in the fern series, and *Lycopodium* among the club-mosses. It is highly probable that these two types, which are very different, represent two quite independent classes derived from different ancestral forms. These ancestral forms may not, however, have differed very much in structure, so far as we can judge, and are most nearly represented at the present time by *Anthoceros*. As we have seen, the sporophyte of the latter is relatively long-lived, growing for many months and developing a complete photosynthetic apparatus, and like the pteridophytes it has an almost independent sporophyte, except for the lack of external organs, leaves, and roots. In *Anthoceros* a relatively small part of the sporogonium is devoted to spore formation, and there is a certain suggestion of the sporangium or spore-bearing organs of the pteridophytes.

**Bower's Theory of Sterilization.**—The importance of the progressive sterilization of the sporoge-

nous tissues in the evolution of the structures of the sporophyte has been particularly emphasized by Professor Bower, who has recently treated this subject at length. (See his recent book, "The Origin of a Land Flora.")

Of the living ferns there is no question that *Ophioglossum* approaches more nearly than any other the hypothetical type suggested by comparison with *Anthoceros*. In this fern the spore-bearing spike (Fig. 12, B) shows very poorly differentiated sporangia, the whole being comparable with some *Anthoceros* type in which the segregation of the spore-masses was more complete than in the existing species.

The club-mosses bear the sporangia singly, each sporangium being subtended by a leaf, and these "sporophylls" together often form a cone or "strobilus." In the ferns the leaves are large and the leaves bear, as a rule, very numerous sporangia. Bower thinks that the ferns may also be considered to represent a modification of the strobiloid type, but there are strong objections to be brought against this view. The cone in the horsetails is also of a very different type from that of the club-mosses, and probably is a quite independent development. It seems to the writer that the assumption of an entirely separate origin for the type of sporophyte found in the club-mosses and ferns is indicated by the data now available.

**Seed-bearing Ferns.**—The great importance of

the pteridophytes in the Paleozoic flora is well known. From the Devonian, where the first fern-like remains are met with, they increase in importance, culminating in the Carboniferous. The richness of the Coal-flora in pteridophytes is sufficiently familiar. It is now known that many of the supposed Paleozoic ferns were really seed-bearing plants which have very appropriately been named "Pteridosperms"—seed-ferns—and some enthusiastic students of these plants have gone so far as to doubt the presence of any true ferns during the Paleozoic, a view which it is hardly necessary to say is hardly likely to prove correct, unless we suppose that these seed-ferns originated spontaneously and had no ancestors.

**Distribution of Living Pteridophytes.**—It is usually taken for granted that the pteridophytes of the present day are mere remnants of the rich Paleozoic flora; but a study of the distribution of the existing ferns shows that this is not the case. It is true that the living horsetails are very degenerate descendants of their Paleozoic ancestors, and the same may be said to a lesser degree of the club-mosses. The case of the true ferns, however, is quite different. The fern types characteristic of the earlier geological epochs have largely disappeared, although there are some ferns, especially in the tropics, which have changed very little from their ancient forebears. These ancient types have been largely replaced by ferns which are better adapted to modern

conditions. These new types of ferns have proved themselves to be much more plastic than the other pteridophytes, and many types have arisen which are extremely well adapted to existing conditions.

In some especially favorable regions, such as the higher mountains of Jamaica, and in New Zealand, the number and variety of the ferns is extraordinary; and they are perhaps the most numerous and conspicuous plants that one encounters. From the tiny filmy ferns, sometimes less than an inch in height, to the majestic tree ferns raising their magnificent crowns of fronds thirty or forty feet above the ground, every available spot is occupied by a bewildering variety of these beautiful plants. Moisture-loving plants as they are, one finds that they become scarcer in the drier parts of the world, but many species have become adapted to dry regions. For instance, there are a number of ferns found in the coast regions of California, where for months during the long rainless summer they become completely dried up, and apparently lifeless, but promptly revive with the advent of the first autumn rains. In the moister and warmer regions many ferns become epiphytes and grow upon the trunks and branches of trees. These epiphytic ferns are among the most beautiful growths that one encounters in the tropics. A few species of ferns are also aquatic in habit, but the number of these water ferns is small.

**Persistence of Ancient Types.**—As is so frequently the case, the most specialized of these ancient types have disappeared before their still more perfect descendants, while the lower and less specialized forms have persisted or have left descendants which have been able to occupy a place to which more highly specialized types are not so well adapted. Thus the tree-like pteridophytes of the Paleozoic have given way to the more perfect modern types of trees, the tree-ferns alone at the present day reminding us of their past glories. But the smaller ferns and club-mosses have been able to compete very successfully with the humbler flowering plants covering the floor of the forest, or draping the banks and hillsides in the moister parts of the world.

The fossil record bearing on the history of the ferns and their allies is remarkably complete, and we know from a study of the fossil forms that all of the most important of the living types, i.e., ferns, horsetails, and club-mosses, were clearly differentiated during the Devonian, and possibly even earlier. Some of the early fossil types have persisted with comparatively little change down to the present time, while in others the changes have become very marked and the earlier types have been largely displaced by their modified descendants, some of which have adapted themselves very satisfactorily to existing conditions even in the temperate regions. Some species, like the field horsetail and the bracken fern,

are very hardy and persistent, and in the more favorable conditions of the moist tropics, ferns constitute an important feature of the vegetation, and some of the modern tree-ferns probably equal in size any of their Paleozoic prototypes.

## CHAPTER V

### SEED-PLANTS

#### THE MODERN PLANT TYPE

**A**S the primitive land plants adapted themselves more and more perfectly to the increasingly diverse conditions associated with their new environment, the evidences of their aquatic ancestry became less and less apparent, and finally in the highest of all plant types, the flowering plants or seed-plants, all indications of their derivation from aquatic ancestors have quite disappeared.

**Mosses and Ferns, Transitional Forms.**—The mosses and ferns illustrate the transitional stages through which the seed-plants, or as these are often called, the “Phanerogams,” have passed in the course of their evolution from their primitive aquatic ancestors, the green algæ. It is evident that the course of this evolution has proceeded along several quite different lines. In the mosses, or bryophytes, the history of the gametophyte, or sexual phase of the plant’s development, illustrates the limitations of this aquatic organism in adjusting itself to the radically different water conditions to

which land plants are subjected. These limitations are probably due to the fact that the gametophyte of the archegoniates is essentially a water plant. Even the most perfect gametophytes, such as are found in the higher liverworts and mosses, owing to their failure to develop an adequate root system and efficient mechanical or supporting tissues, are unable to attain any but the most modest dimensions. Moreover, these plants are essentially amphibious, as water is necessary to effect fertilization.

In the ferns the development of the race centers in the sporophyte or neutral generation. The sporophyte, being the product of the fertilized ovum, is equivalent to the zygote or sexually developed resting spore of the ancestral green algæ from which the mosses and ferns are descended. As the zygote of these algæ is usually adapted to survive drought, we may say that the sporophyte has never been an aquatic structure, but from its earliest beginning is an organism fitted for terrestrial existence. It evidently possesses a potentiality for development on land that is not shared by the essentially aquatic gametophyte. It might be said that nature, having in the mosses exhausted her resources in the endeavor to transform the aquatic gametophyte into a successful land plant, turned to the spore-bearing generation as a more promising subject for experimentation. In the ferns there is encountered, then, for the first time, a sporophyte which possesses true roots having sufficient capacity for water absorption

to enable it to supply the water necessary for the further development of the sporophyte, which now becomes a perfectly developed land plant, with stem, roots, and leaves and elaborately developed tissues.

With the elaboration of this sporophyte, or terrestrial phase of the plant's life, there has been a gradual reduction of the aquatic phase, and the gametophyte becomes more and more insignificant, culminating in the condition met with in the heterosporous pteridophytes, in which the sex of the future gametophyte is already indicated by the character of the spore. This tendency to heterospory is shown clearly in several quite independent lines, and just as the different types of sporophytes, i.e., ferns, horsetails, and so on, probably have arisen independently, so heterospory also developed in various quite different lines. In some of these, e.g., the water ferns, no further advance seems to have been made; but in other groups a further development of heterospory resulted in the formation of seeds, the distinguishing mark of the highest plants. As was pointed out in the last chapter, the seed is not a new organ, but is merely an elaboration of one which already existed, the megasporangium, or the sporangium in which the large spores or megaspores are developed, and from the latter the female gametophyte is produced. There is abundant evidence from a study of the Paleozoic pteridophytes that seeds developed in several widely separate groups, and this, together with the structure of the

living seed-plants, makes it pretty certain that the existing seed-bearing plants have not all arisen from the same stock.

**Selaginella.**—Of the existing pteridophytes one genus of club-bosses shows a remarkably close approach to the seed-bearing condition, and illustrates very beautifully the intermediate stage between the typical pteridophytes and the lowest seed-bearing plants. In these club-mosses (Fig. 14, A) we have seen that the germination of the megaspore is almost entirely completed while the spores are still contained within the sporangium, and the growing gametophyte is nourished by food substances derived directly from the cells of the sporophyte, and not from materials stored within the spore itself, as is the case in the other pteridophytes. The final stages, however, including fertilization, are completed after the spores are set free, and as in the lower pteridophytes, water is necessary to convey the sperms to the open archegonium.

If we examine the “flowers” of one of the lower seed-plants, such as a fir or pine (Fig. 15, B), we shall find that they are composed of closely set scale-like leaves arranged in a cone which is very much like that of the club-mosses. These cones are of two kinds, one bearing megasporangia like those of *Selaginella*, and usually denominated “Ovules,” the other bearing the microsporangia or “Pollen-sacs.” In the pine there are two ovules borne upon each scale of the young cone, and

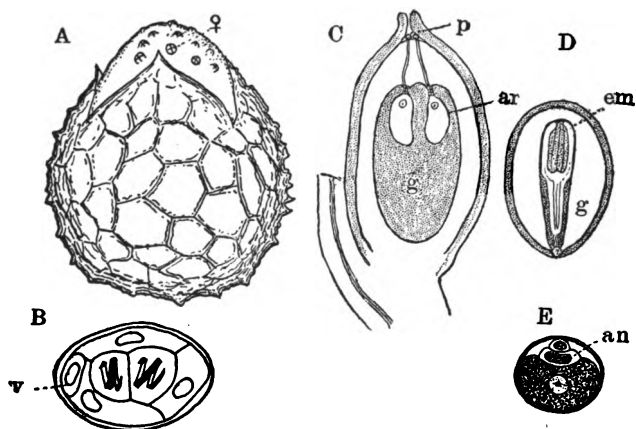


FIG. 14

Comparison of the gametophytes of heterosporous Pteridophytes and Gymnosperms.

A—Germinating megaspore of *Selaginella*, showing the enclosed female gametophyte, ♀, protruding from the ruptured spore apex.

B—Section of a microspore of *Isoetes*, showing the very much reduced male gametophyte within, v, vegetative cell of gametophyte; two sperms can be seen in the section.

C—Section of megasporangium (ovule) of a pine. A single megaspore is present, within which is the female gametophyte, g, with the archegonia, ar. Two microspores (pollen-spores) are present in the chamber at the apex of the ovule. These have sent down the pollen tubes.

D—Section of the ripe megasporangium (seed). Within the hard shell is the gametophyte, g, enclosing the young sporophyte, em, derived from the egg.

E—Microspore (pollen-spore) of *Cycas*; from the antheridial cell, an, two large ciliated sperms are developed.

a study of their development shows that their essential structure is very much like that of the

megasporangium of *Selaginella*. Usually but one spore matures, but this is very large, and within it arises the gametophyte very much like that in the megaspore of *Selaginella*, and, like it, producing a number of archegonia. The megaspore, however, is never set free, but remains permanently within the ovule, and this necessitates a quite different method of fertilization (Fig. 14, C).

The microsporangia of the pine are also in pairs, but are upon the lower side of the sporophyll or scale which bears them. The development of the microsporangium follows very closely that of *Selaginella*, and the spores are formed in groups of four, as in all the archegoniates. These microspores, or "pollen-spores" (Fig. 14, E), give rise to a rudimentary male gametophyte with two sperms, which are, however, destitute of cilia. When the ripe pollen-spores fall upon the apex of the ovule they germinate, sending out a slender tube which pushes its way through the tissues overlying the apex of the megaspore, and the two sperms, or generative nuclei, pass into the pollen-tube and are thus conveyed to the archegonium. The development of the pollen-tube does away with the necessity of water for effecting fertilization, and the last evidence of the aquatic origin of these plants disappears.

**Motile Sperms in Seed-plants.**—One of the most important discoveries of recent years is the fact that in a number of the lowest seed-plants fertilization

is still effected by large motile sperms very much like those of the ferns. The only plants in which this has been found are the fern-like cycads, including the so-called "sago palm" of the greenhouse, and the curious Ginkgo, or maiden-hair tree, which is not uncommon as an ornamental tree. Both of these types had long been recognized as being very ancient ones and as having very close resemblances to the ferns, and the discovery that they both develop these motile sperms practically makes this relationship certain. In both the cycads and Ginkgo, the female gametophyte is not essentially different in its structure from that of the pine or *Selaginella*, and the pollen grain, after it has fallen upon the ovule, also develops a pollen-tube as it does in the pine. This pollen-tube, however, becomes greatly distended by an accumulation of water and finally bursts, discharging the two enormous sperms, together with the water, into the chamber which lies above the archegonia. So we see, even among the seed-plants, there may still be this same aquatic type of fertilization that obtains in the whole of the archegoniate series from which these plants have sprung. In a Cuban cycad, which has recently been described by Caldwell, there may be as many as sixteen sperms developed in one pollen-tube.

In the pine and other similar types, the pollen-spore, in which the germination is well advanced at the time the spore is shed, shows a division into

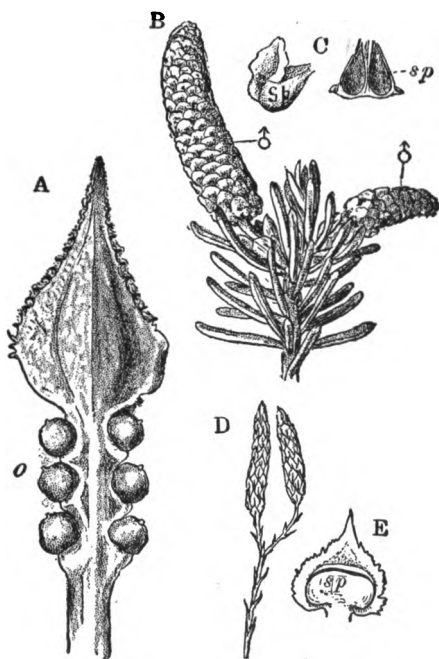


FIG. 15

A—Megasporophyll of *Cycas*, with six megasporangia, or ovules, *o*.

B—Two microsporangial cones of a spruce.

C—Two views of a sporophyll showing the two sporangia, or pollen-sacs, *sp*, upon its lower face.

D—Two cones of a club-moss, *Lycopodium*, showing a marked superficial resemblance to the cones of the spruce. The sporophyll, E, has a single sporangium upon its upper side.

several vegetative cells and an antheridial cell. The germinating spore sends out its pollen-tube, which

penetrates the tissue overlying the embryo-sac very much as the fungus bores its way through the tissues of its host. In many of the conifers there is an interim of nearly a year between the time of pollination and the penetration of the pollen-tube into the archegonium, which is formed long after the pollen first falls upon the ovule.

**Fertilization.**—With the discharge of the sperm nucleus into the egg, and its fusion with the egg-nucleus, fertilization is consummated, and the egg develops into the embryo-sporophyte, which at once begins to grow until the young organs—stem, roots, and leaves—are well advanced. As is the case in *Selaginella*, only a portion of the egg develops into the embryo proper, a greater or less amount going to form a peculiar organ known as the suspensor, which pushes the developing embryo into the mass of gametophytic tissue, the “endosperm,” whose cells are filled with starch, oil, and albuminous reserve food for the needs of the young sporophyte when the seed germinates (Fig. 14, D). The wall of the sporangium, together with the accessory envelopes, or integuments, which are found in nearly all seed-plants, hardens and forms the characteristic shell, or testa, upon the outside of the seed. It is thus clear that the seed is not a new formation, peculiar to the seed-plants, but is a more or less perfectly changed megasporangium, within which is contained the megaspore with its enclosed gametophyte, in which in turn is embedded the embryo-

sporophyte, so that the ripe seed comprises structures belonging to three generations.

**Advantages of the Seed Habit.**—The advantages of the seed habit are apparent, and it is evident that this has resulted in a type of plant peculiarly adapted to life on land. This is shown by the extraordinary development of seed-bearing plants at the present time. Among the pteridophytes, except in *Selaginella*, which is probably the highest genus of living pteridophytes, the developing gametophyte is exposed to the vicissitudes of an uncertain water supply, free water being essential to its development and for fertilization. In the seed-plants the gametophyte is largely protected during its development, receiving its water supply indirectly through the tissues of the sporophyte, and water is no longer necessary for the fertilization of the ovum, owing to the formation of the pollen-tube. Moreover, the young sporophyte is very perfectly protected during its early development, and before the seed ripens it reaches a condition where it is ready quickly to assume an independent condition.

The food stored up in the seed during the process of ripening, provides an ample supply of food for the young sporophyte during the early stages of germination. These conditions give the seed-plants a tremendous advantage over most pteridophytes, except under very special conditions, either where the latter have developed extraordinary power of vegetative reproduction,

as, for example, the extensively spreading root-stocks of the horsetails or the bracken fern, and in some of the club-mosses; or where there is a constant supply of moisture, as in many tropical mountain regions or countries like New Zealand. In such favored regions ferns may often constitute an important factor of the flora and hold their own very successfully with the seed-plants.

**The First Seed-plants.**—The lower types of seed-plants are mostly trees or shrubs whose resistant tissues have in many cases been preserved in a fossil state in an astonishingly perfect manner, and consequently the geological record is especially satisfactory in regard to these important forms. A study of these fossils shows that the seed habit arose at a very early period. The earliest seed-bearing plants were very different from any living types, and they have been separated as a separate order, known as the Cordaitales. The affinities of the latter with other plants are extremely doubtful, and it is a question whether they are related at all to any existing species. The Cordaitales are found as far back as the Devonian, and possibly even earlier, and were especially abundant during the Carboniferous. They became quite extinct before the end of the Paleozoic.

**Origin of Seed-plants.**—The fern-like plants, which are first certainly evident in the Devonian, where many forms flourished, like all of the types of pteridophytes had an extraordinary develop-

ment during the Carboniferous. Recent studies of these Carboniferous "ferns" show that many of them were really intermediate in character between the true ferns and the cycads, and many of them produced true seeds, hence the very proper name of Pteridosperms, or seed-ferns, applied to these. It is highly probable that from some of the pteridosperms the cycads are directly descended, and perhaps also the curious Ginkgo, which has been referred to, whose sole representative now flourishes in the temple gardens of China and Japan, and occasionally is seen in our parks and gardens. The great variety of these seed-bearing ferns indicates that the seed habit was developed in more than one line of ferns, just as in the living ferns, the two heterosporous families, the Marsiliaceæ and Salviniaceæ, are of obviously independent origin.

Among the fossil club-mosses of the Carboniferous, there are also unmistakable evidences of seed-bearing genera, such as *Lepidocarpon*, which presumably was related to the great tree-like *Lepidodendrons*. In many ways these seed-bearing club-mosses suggest the peculiar conifers of the Southern Hemisphere, *Araucaria* and *Agathis*, and it is not impossible that the prevailing modern Gymnosperms, the conifers, are the descendants of some of the tree-like Paleozoic club-mosses. It must be noted, however, that this view is strongly opposed by some eminent students of the Paleozoic fossils.

The curious horsetails, or scouring rushes, belonging to the genus *Equisetum*, are the sole survivors of a class, which in the early geological formations was represented by a great variety of forms, some of which attained tree-like dimensions. Some of the fossil species were heterosporous, but there is no evidence that any of them advanced far enough to develop seeds, and so far as we know the seed habit was never attained by members of this class of pteridophytes.

**Gymnosperms and Angiosperms.**—The seed-plants, as they now exist, are commonly divided into two very unequal classes, the Gymnosperms and the Angiosperms. The gymnosperms, which include the cone-bearing evergreens, are the older type, and in these the gametophyte shows obvious resemblances to that of their pteridophytic forebears, and the homologies are sufficiently evident. The angiosperms, on the other hand, the ordinary flowering plants, which comprise an overwhelming majority of existing seed-plants, show much less evidence of their origin from lower forms, and at present it is an open question whether or not they are at all related to any of the existing gymnosperms. It is, moreover, very unlikely that all of the existing gymnosperms have had a common origin. The two lowest types, the cycads and Ginkgo, are, with very little question, descended from fern-like ancestors, presumably through some types of the seed-bearing ferns of the Carboniferous. This is certainly true

of the cycads, which both in form and internal structure reveal unmistakably their fern ancestry. Moreover, the discovery of fern-like sperms in these, and the actual development of green tissue in the gametophyte under certain conditions, show that they are very much less reduced in these respects than some of the living heterosporous pteridophytes, and indicate still further the extremely primitive nature of these low seed-bearing plants.

In the conifers, the adaptation to terrestrial conditions is complete, and all trace of their aquatic ancestry is finally lost. These are the predominant type of gymnosperms at the present day, and are not certainly met with until the last of the Paleozoic formations, where in the form of some Permian species there is evidence of the beginning of the coniferous series. As we have already indicated, there is some reason to suppose that these conifers may be descendants of some of the gigantic club-mosses of the Carboniferous, but some eminent authorities believe that the conifers also are descended from fern-like ancestors.

**Gnetales.**—The last order of the gymnosperms, the Gnetales, is a small one containing three very peculiar genera, with a small number of species, evidently not at all closely related either to each other or to the other gymnosperms. Unfortunately these plants are practically unknown in a fossil condition, and at present it is impossible to determine their exact position in the system.

**The Gymnosperms Not a Homogeneous Class.**—From the above statements it is evident that the gymnosperms do not constitute a homogeneous assemblage of plants, but represent a more or less heterogeneous collection of forms, which may very well represent several quite unrelated lines of descent. They all agree in having seeds of a primitive type, usually exposed upon open leaves, or sporophylls; whence their name of Gymnosperms, or “naked-seeded” plants. They are evidently less fitted to existing conditions than their rivals, the angiosperms, which have largely superseded them and have shown a far greater power of adaptation, clearly indicated by their enormously greater variety of species and individuals. Probably there are not more than five hundred living species of gymnosperms, while of the angiosperms more than one hundred thousand already have been described.

#### THE CYCADS

During the Paleozoic, especially in the Carboniferous, there arose a great assemblage of fern-like plants, showing a wide range of structure, many of them approaching both in the structure of the tissues and in their reproductive parts the lower types of seed-bearing plants. Some of these pteridosperms, or seed-bearing ferns, were evidently not very different in appearance from some of the living ferns, especially those belonging to a small

order of mostly tropical ferns, the Marattiaceæ, with which there is little question that they are directly related. Others were more like the lowest of the existing seed-plants, the Cycads, and were probably the direct progenitors of the latter. The cycads become more important in the later Paleozoic formations, but reach their maximum development in the next great geological epoch, the Mesozoic.

The predominance of cycads in the early Mesozoic suggests that the climate of that period very materially differed from that of the Carboniferous. The rank growth of pteridophytes at that time must have been conditioned by an excess of moisture, and a probably very even temperature. The modern cycads are for the most part plants of the sub-tropical and drier tropical regions, where they are usually subjected to more or less extended periods of drought. It may be that increasing dryness was one cause of the tendency to seed-formation in the later Paleozoic time. It is true that there was one group of seed-plants, the Cordaitales, already well developed, which became extinct before the end of the Paleozoic, while, as we know, seeds were developed in various of the fern-like plants and in the club-mosses. But there is some evidence that even during the Paleozoic there were fluctuations in the amount of moisture, and it is possible that these fluctuations may coincide to some extent with the periods of seed formation.

The cycads have now given place largely to the

more modern types of seed-plants, but there are still some seventy-five species of these, pretty well distributed over the warmer parts of the earth. Of these, the genus *Cycas*, represented by the common *C. revoluta*, the "Sago Palm" of the florist, is especially interesting, as it is a survivor of one of the earliest genera known, and has come down probably from the early Mesozoic with apparently little change. *Cycas* is in habit very much like a tree-fern. The upright trunk bears at its summit a crown of fern-like leaves, which when young have the leaflets coiled up like those of a young fern-leaf. The fertile leaves, or sporophylls, in *Cycas* retain the fern-like form (Fig. 15, A), and the enormous ovules, or megasporangia, are borne on the margins of the sporophylls, and later develop into great seeds, which in some species are as big as a hen's egg.

Although the gametophyte is well advanced in the big seeds, its final development and fertilization take place after the seed has fallen off of the plant. The gametophyte has also been known in some cases, where fertilization was not effected, to continue its growth and develop a green mass of tissue like the gametophyte of the lower ferns, indicating that as heterospory developed in the fern ancestors of the cycads, the reduction of the gametophyte was much less than in that of the existing heterosporous ferns. This great development of the gametophyte, together with the presence of motile

sperms, emphasizes the very low rank of these primitive seed-plants.

**Cycadeoideæ.**—Either from the cycads, or perhaps independently from some of the Paleozoic pteridosperms, there arose a second group of cycad-like plants, which also culminated in the Mesozoic, and were much more specialized than any of the true cycads. These plants have been called “Cycadeoideæ,” and the most important collections of these have been made from the Black Hills region of Dakota and Wyoming. From a study of these fossils (for details see Wieland: “American Fossil Cycads”), which have been very well preserved, our knowledge of the structure of these remarkable forms is very complete. In some of these Cycadeoideæ the “flowers” have been very well preserved, and the arrangement of the sporophylls, which are borne together upon the same cone, is so much like that of such flowers as the water-lily or magnolia, that some students have actually claimed that these Cycadeoideæ are the real ancestors of the higher flowering plants, the Angiosperms. It must be remembered, however, that the Cycadeoideæ are gymnosperms, that is, the naked seeds are borne free upon the sporophylls and the “stamens” are very unlike those of the angiosperms, and closely resemble the leaves of the true ferns. Moreover, it may be assumed that the gametophyte was well developed, like that of the cycads, and it would certainly be rash

to assume a direct connection between these forms and any of the higher plants, until we have a great deal more evidence upon the subject. Nevertheless, the possibility of an origin of the higher plants from some gymnospermous forms, allied to the cycads, must be borne in mind in any speculations as to the origin of the angiosperms.

### GINKGOALES

The curious maiden-hair tree, or Ginkgo, which we have already referred to, is the sole survivor of an extremely ancient race which was represented by many species in the later Paleozoic and early Mesozoic, some of the later Paleozoic species having actually been referred to the existing genus Ginkgo. In the temple gardens of Japan are many superb specimens of this strange tree. These are sometimes of great size, and are said to be many centuries old. Unlike the cycads, the tree is extensively branched, and looks not unlike a poplar. Its curious fan-shaped leaves, which are deciduous, show a forked venation like that of a maiden-hair fern; hence the name, "maiden-hair tree," sometimes applied to it.

The large seeds, which are borne at the end of short branches, are much like those of *Cycas*, and the structure of the gametophyte and the development of large motile sperms in the pollen-tube are strikingly similar. It seems probable that there is a real relationship between Ginkgo and the cycads, but it

is probably a remote one. There does not, however, seem to be any strong evidence of any direct relation with any other existing plant, although formerly Ginkgo was associated with the conifers, and there are some undoubted resemblances between them, such as the character of the wood and the seed. For a long time it was supposed that the tree was extinct in a wild condition, but it has finally been discovered growing wild in certain parts of western China.

#### CONIFERALES

The great majority of the living gymnosperms are Conifers, the ordinary cone-bearing evergreen trees, which in certain regions, like the Pacific Slope of North America, are the dominant forest trees. There is much difference of opinion as to the origin of the conifers, but we believe that the weight of evidence is in favor of their derivation from some types allied to the tree-like club-mosses of the Paleozoic. The great club-mosses, like *Lepidodendron* and *Sigillaria*, although they were undoubtedly different in many ways, nevertheless recall in certain respects the modern coniferous trees. Like the latter, they developed a secondary growth in thickness, and the cones are quite similar. As some of these Paleozoic club-mosses are known to have developed seeds, which recall those of the living *Araucaria*, the derivation of the latter

from such seed-bearing lycopods is by no means improbable. This is, however, by no means so obvious as the derivation of the cycads from fern-like forms; but if it should be demonstrated, of course it would indicate that the two orders of gymnosperms—conifers and cycads—are absolutely unrelated. Some students of the fossil gymnosperms consider the Cordaitales, which are the oldest of all known seed-plants, to be a composite type with affinities both with conifers and cycads; but the arguments brought forward in favor of this theory are not entirely convincing, and it is quite as likely that there is no direct relationship between the Cordaitales and any living gymnosperms.

The earliest known Conifers, which were probably allied to the living genus *Araucaria*, which includes the Norfolk Island pine, are met with in the later Paleozoic, from which time they increase rapidly in number and importance, until by the end of the Mesozoic, practically all of the existing genera are met with. With the advent of the angiosperms, which began to be prominent by this time, the conifers decline in importance but still have held their own pretty well, and are important constituents of the floras of many parts of the world; but their importance is due rather to number of individuals than to any great variety of species. The conifers have shown themselves to be far more adaptable than the cycads, which at present very seldom occur anywhere in large numbers, while the

conifers, being very frequently gregarious in habit, may form almost perfectly pure forests of a single species.

The most obvious difference between cycads and conifers is the different relation of stem and leaves, the same that distinguishes the ferns and club-mosses. The simple, or sparingly branching palm-like trunk of the cycads, with its crown of fern-like fronds, is extremely different from the extensively branched conifer, with its scattered, slender, and often needle-shaped leaves. Most of the more familiar conifers, like the pines and firs, are more or less markedly xerophytic, i.e., their foliage is adapted to check excessive transpiration. This may be correlated with their growth in dry regions where they are exposed to the hot sun, or it may be in the case of the Northern species an adaptation to prevent loss of water during the winter, a condition which the Northern angiospermous trees meet by casting their leaves. Species growing in moister regions have softer and broader leaves, and this is noticeably the case in some of the presumably more primitive types, like *Araucaria* and the Kauri pine of New Zealand, which have relatively broad leaves and are decidedly less xerophytic in habit than the pines and spruces of the North. While most of the conifers are evergreens, a few, like the larch, and the bald cypress of the Gulf region, cast their leaves in autumn, behaving thus like deciduous angiospermous trees.

Some conifers are quite adaptable, certain species growing under very unfavorable conditions, like the pines and firs of the alpine summits of the Sierras and Rocky Mountains, or the barren slopes overlooking the desert. A few species, like the Monterey pine and cypress, grow where they are exposed to the full force of the ocean winds. They reach their finest development on the western slopes of the great mountain chains bordering Pacific North America, and are also highly developed in the Manchurian and Japanese region on the other side of the Pacific. The conditions of the Pacific slope of North America seem to be better fitted for the needs of the coniferous trees than those of any other part of the world. A very temperate and uniform climate, with abundant moisture, especially towards the north, perhaps represents to some extent the climatic conditions of the later Mesozoic and the earlier Tertiary, when the ancestors of the present coniferous flora flourished; and the giants of the vegetable kingdom have developed in these Pacific forests. The mighty Sequoias, the last of their race, tower above all the other trees of the forest; but giant pines, firs, and cedars, which accompany them, are unrivaled in size except by the Sequoias, and make up a forest that is unequalled in all the world.

That some of these conifers, like the Sequoias and wild nutmegs of the California forest, or the cypresses of the southern swamps, were once widespread trees is plainly shown by the fossil remains

in many regions both of the Old and New World, where it would be quite impossible for them now to exist. Great changes must have taken place in the climate since the time when these trees were common over much of the Northern Hemisphere, where now they maintain only a very precarious existence in a few places where unusually favorable conditions have permitted them to survive.

#### GNETALES

Distributed through the Tropics of both the Old and New World, there are found about a dozen species of trees and woody climbers belonging to the genus *Gnetum*. Some of these are lianas, climbing to the tops of lofty trees. The opposite, oval, pointed leaves are net-veined like those of the typical dicotyledons, and the flowers, borne in catkin-like spikes, may be compared to those of a poplar or willow. The plant, however, is "gymnospermous"; that is, the seeds are not contained in an ovary, and in this respect they agree with the conifers and cycads; but otherwise *Gnetum* has little in common with the other gymnosperms, nor is its relationship to the other genera, *Ephedra* and *Welwitschia*, which are associated with it to form the order, *Gnetales*, at all certain. *Gnetum* is sometimes held to be intermediate between gymnosperms and angiosperms, but the evidence for this is by no means decisive.

The second genus of Gnetales, *Ephedra*, with some twenty species, is represented in the United States by two or three species of the arid Southwest. In the Colorado desert, and the deserts of southern Arizona, one frequently meets with these straggling bushes, whose leafless, gray-green, jointed stems, remind one of the horsetails. While these bushes are very different in aspect from most conifers, the structure of the seeds is quite similar, this being especially the case with the highly developed gametophyte.

The third genus of the Gnetales, *Welwitschia*, has but a single species, confined to a limited desert region in Western Africa. This extraordinary plant has a short, thick trunk, tapering into a long tap-root, so that it looks like a great carrot or parsnip with the top cut off. Growing from the margin of the flattened trunk-apex are two immense strap-shaped leaves, which are all the plant has. From the margin of the trunk cones of flowers are also produced. These are made up of large red scales, which are very conspicuous, and, it is said, attract insects so that the plant is sometimes, at least, cross-pollinated. The more recent studies on this plant by Professor Pearson, of Cape Town, indicate certain resemblances in structure to *Gnetum*, and it is not impossible that the two genera are remotely related. *Ephedra* probably is not related to either of the other genera. Practically nothing is known of the geological history of the Gnetales, but their

present distribution indicates that they are probably pretty old types.

### RÉSUMÉ.

**Seed-plants Not All of Common Origin.**—That the seed habit developed a number of times in quite unrelated groups of pteridophytes is amply shown by the fossil remains of seed-bearing plants in the Paleozoic. Some one, or perhaps more than one, of the seed-bearing ferns were probably the progenitors of the existing cycads, and some of the more specialized cycad-like forms of the Mesozoic formations. It is also pretty certain that the peculiar genus *Ginkgo* is also descended from some fern-like Paleozoic type. The cycads of the present time are much scattered, and seldom occur in numbers to make them important constituents of a flora. The existing types are descended from some of the less specialized fossil ones.

The conifers are decidedly the prevailing type of gymnosperms at the present day. Although the number of known species is less than four hundred, they are nevertheless very important factors in the existing flora of many parts of the world, as they often form extensive forests, including the largest of known trees. The order is an adaptable one, and conifers grow under quite different conditions; but there are no real aquatic forms, though some, like the cypress and tamarack, are swamp

trees. The origin of the conifers is uncertain, but there is some reason to assume a descent from forms allied to the giant club-mosses of the Coal Measures. The affinities of the other order of gymnosperms, the Gnetales, are not at all clearly established, nor is it certain that the three known genera are related among themselves. There is some ground for an assumption of a relationship between some of these and the lower angiosperms; but the origin of the latter, the predominant modern type of plants, is very far from clear.

**The Living Seed-plants Not All Related.**—It is, however, extremely likely that the existing seed-bearing plants do not form a homogeneous class, but more properly should be considered as a class representing several quite independent developmental lines, some of which may not be related at all. The lower types, or gymnosperms, show evident relationship with the pteridophytes, but the different orders may very well have been derived from quite different pteridophytic stocks. The origin of the modern type of flowering plants, the angiosperms, is exceedingly obscure. One group of seed-plants, the Cordaitales, the earliest known type, became extinct at the end of the Paleozoic, and probably has left no descendants.

## CHAPTER VI

### THE ANGIOSPERMS

**T**HE evolution of the seed marks the final step in the complete adjustment of the plant organism to strictly terrestrial existence, and while seeds undoubtedly arose independently in several widely separate classes, most of these primitive seed-plants have disappeared completely, or have left only a few descendants, which maintain a more or less precarious existence at the present time. One line of seed-plants, however, has proved itself eminently adapted to modern conditions, and constitutes an overwhelming majority of living plants. These prevailing flowering plants of the present time are known as Angiosperms. In the angiosperms the plant organism reaches its most perfect expression, and they now dominate the land floras of all parts of the world. Plastic to a degree unequaled by any other plants, they have succeeded in adapting themselves to the most diverse conditions. In the burning deserts of the Tropics, at the utmost limits of vegetation in the polar zones, and on mountain summits, angiosperms have made themselves at home. Some have even invaded the sea, while still others are inhabitants of fresh-water marshes or are sub-

mersed in lakes or rivers. Like the fungi, many angiosperms are parasites or saprophytes in their habits, and like the fungi these may be quite destitute of chlorophyll, and must, therefore, depend upon other organisms for their supply of organic food.

**Adaptability of Angiosperms.**—Perhaps in no way is the adaptability of the angiosperms better shown than in their relation to the animal world. Serving as plants do for the food of a vast number of animal forms, there have been evolved, in the course of the development of both the animal and plant kingdoms, numberless cases of special adaptations of which the plants have taken advantage. This is seen perhaps most perfectly in the evolution of flowers, whose peculiarities are very generally associated with cross pollination through the agency of insects or birds. The peculiar modifications of the latter, for instance, the mouth parts of bees or butterflies, or the beak of the humming birds or honey suckers, are clearly correlated with floral structures. Many types of fruits also are associated with modifications in animal structures. The teeth of many mammals, and the beaks of certain birds, are undoubtedly adaptations for feeding upon certain types of fruits, and the importance of animals, especially birds, in the distribution of the seeds of many plants is sufficiently well known.

Although it is almost certain that all of the angiosperms have arisen from a common stock, the range

of their structures is extraordinarily great, illustrating again their remarkable powers of adaptation. Some of them are tiny, almost microscopic water plants of extraordinarily simple structure; others are humble weeds, completing their whole life in the course of a few weeks, while still others are giant trees, living hundreds of years. With all this extraordinary variation in size, form, and habit, the fundamental structure of the flower, the characteristic mark of the angiosperms, is very uniform, but is so different from that of any gymnosperms as to make the origin of the angiosperms a matter of great uncertainty.

**Angiosperms Absent from the Early Rocks.**—While the ferns and gymnosperms have left abundant and well-preserved fossil remains whose nature is unmistakable, of the angiosperms, except in the later geological formations, only scanty traces are discernible, and these are often very uncertain in their nature. While a good many fragments of leaves and stems from Paleozoic and early Mesozoic rocks have been assigned to angiosperms, these fragments in most cases are very poorly preserved, and their real nature is, to say the least, problematical. The tendency among recent students of these fossils is to relegate them either to pteridophytes or gymnosperms.

It is not until the later Mesozoic formations are reached that unmistakable remains of angiosperms are found. From the Cretaceous upward

they rapidly increase in number and variety, and many existing genera can be plainly recognized among these Cretaceous fossils. So far as the evidences of geology go, the two great divisions of angiosperms—Monocotyledons and Dicotyledons—seem to be of about equal antiquity, and practically no light is shed on the relationships of these two groups to each other from a study of their fossil remains. Nor are there any evidences of fossil remains intermediate between angiosperms and gymnosperms, unless some of the cycad-like forms of the Mesozoic are to be so regarded, and this at present is at least doubtful. Equally unsatisfactory are the attempts to derive the angiosperms from any of the existing gymnosperm types.

**The Earlier Fossil Angiosperms.**—The sudden appearance of the angiosperms in the Sub-Cretaceous formations, and the close resemblance of these earliest fossils to living forms, makes it quite likely that the earliest angiosperms have left no visible traces in the rocks. This may be due either to the perishable nature of these primitive forms, which were, perhaps, delicate herbaceous plants, like many of the existing monocotyledons, or such low dicotyledons as the buttercups and some of the peppers; or it may be that the primitive forms lived in relatively dry localities where the conditions for fossilization were not favorable.

**The Flower.**—The flower of the angiosperms is a much more highly developed structure than that

of the gymnosperms. In the latter the resemblance of the sporophylls to the spore-bearing leaves of

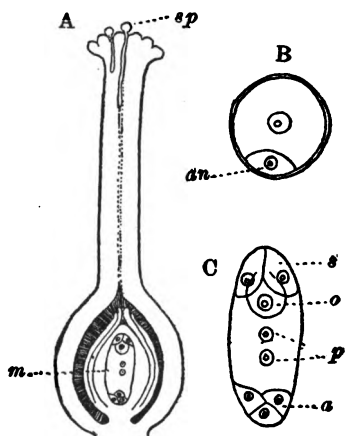


FIG. 16

A—Diagram of simple pistil of an Angiosperm, composed of a single carpel or sporophyll. The upper part forms the “stigma,” or receptive surface, upon which the pollen-spores, *sp*, germinate. The pollen tubes traverse the elongated “style,” before they reach the ovule, or megasporangium, within the enlarged cavity, or “ovary,” formed by the base of the carpel. Within the ovule is born a single large spore (*m*), the “embryo-sac.”

B—Ripe pollen-spore, showing large sterile cell, and antheridial cell, *an*.

C—The megaspore, or embryo-sac, shown in A, *m*, with the enclosed gametophyte reduced to eight cells. At the upper end, the egg-apparatus consisting of two synergids, *s*, and the egg-cell, *o*; at the base three “antipodal” cells, *a*; in the middle the two “polar” nuclei, *p*.

the pteridophytes is very plain. In the angiosperms the sporophylls are very much more altered.

The microsporangia, or pollen-sacs, are borne upon much modified sporophylls called stamens, and the leaves known as carpels, from which are developed the ovules, or megasporangia, are also greatly altered. The carpels form a closed cavity, the ovary, within which the ovules are placed so that they are effectively protected during the development of the seed. The flowers also possess in many cases showy leaves, forming the floral envelopes. The ovules are not strikingly different from those of the gymnosperms, but there is usually a second integument.

**Origin of the Angiosperms Doubtful.**—There are undoubtedly certain points in common between the Gnetales and the angiosperms, this being especially the case in the genus *Gnetum*; but as we have already seen, the Gnetales are very doubtfully related to the other gymnosperms, so that even if it should be shown that there is a relation between the Gnetales and the angiosperms, this would not help much in explaining the relation of the latter to lower forms. Some of the monocotyledons, especially the palms, bear a superficial resemblance to the cycads; but this is probably only a parallelism, and does not indicate any real relationship.

**Gametophytes of the Angiosperms.**—The pollen-spores of the angiosperms are not materially different in structure from the microspores of the heterosporous pteridophytes or the pollen-spores of

the gymnosperms. The male gametophyte is also very similar to that of many gymnosperms. The very slight change shown in the evolution of the microspore is remarkable. There is little difference structurally between the pollen-spore in the highest seed-plant and the spore of the humblest liverwort.

The development of the megaspore shows many analogies with that of the gymnosperms, and the early development of the female gametophyte is very similar. The early stages of germination in the embryo-sac are quite similar to those in the pine or *Selaginella*; but the nuclear divisions are much less numerous, so that in the normal embryo-sac, at the time it is fertilized, there are only eight nuclei, representing as many cells, of the extremely reduced female gametophyte; or in some cases there may be only seven nuclei, as there is a fusion of two of the original nuclei (Fig. 16, C).

There has been much discussion as to the homologies of the structures of the embryo-sac in gymnosperms and angiosperms, and the matter is still in dispute. The most marked departures from the ordinary angiospermous type are found in two plants which are in some respects very unlike. In the genus *Peperomia*, a simple dicotyledon which in some ways suggests some of the lower monocotyledons, the gametophyte has sixteen instead of eight nuclei, and this is true also in *Gunnera*; and in the screw-pine (*Pandanus*), a monocotyledon,

there may be 50 or more nuclei at the time of fertilization. In all of these genera, which are usually considered to be primitive types, the occurrence of these different forms of embryo-sac is interesting, as it suggests, at least, a condition intermediate between the embryo-sac of the typical angiosperms and that found in some lower type, possibly a form like *Gnetum*.

It must be borne in mind that this microscopic body within the embryo-sac, composed of eight cells, and the still more rudimentary structure developed from the germinating pollen-spore, are all that remain of the sexual plants or gametophytes, which in the lower archegoniates are so conspicuous. In the angiosperms the plant, as we ordinarily think of it, is the strictly non-sexual sporophyte. The stamens and carpels are not the sexual reproductive organs, the latter being really represented by the rudimentary archegonium in the embryo-sac and the very simple antheridium in the pollen-spore, which correspond to the sexual organs in the mosses and ferns.

**Flowers of the Lower Angiosperms.**—In many of what are usually considered the most primitive angiosperms, e.g., willows, poplars, bur-reeds, screw-pines, and others, the flowers are diclinous, that is, stamens and carpels are in different flowers, and often upon different plants. The flower may even be reduced to a single carpel or stamen, and the floral envelopes, which are so striking a feature

of most flowers, may be quite absent or represented only by inconspicuous scales. There is much difference of opinion as to the nature of these very simple flowers. Some of them may be explained as reductions from a more perfect type; but such an explanation is not satisfactory in the case of other forms, and most botanists believe that the simple characters of many of these "apetalous" flowers are really primitive (Figs. 17, 18).

**The Typical Angiospermous Flower.**—In much the greater number of Angiosperms the flowers are "hermaphrodite," "perfect," or to use the more accurate term, "amphisporangiate," having both stamens and carpels. Moreover, these flowers possess usually a conspicuous floral envelope, which may consist of nearly uniform colored leaves, as in the lilies, or which may be differentiated into a green "calyx" and a highly colored "corolla." There are a number of types, both among monocotyledons and dicotyledons, in which the flower consists of an indefinite number of quite separate parts, the carpels also being entirely free from each other. Such flowers are known as "apocarpous" ones. The magnolia, buttercup, and arrow-head are examples of such apocarpous flowers (Figs. 17, B; 18, C). These flowers show a repetition of parts, especially in the stamens and carpels, while in the more usual floral types there is a definite number of parts with a tendency towards reduction in the number of stamens and carpels, and the carpels are also

usually united into a compound structure, the pistil (Fig. 18, D).

The apocarpous flowers are generally admitted to be primitive types, but whether all of the diclinous flowers are reduced from such types, having both stamens and carpels, is another question. It seems more in accordance with the data at hand to assume that in the primitive angiospermous stock there were developed both monosporangiate and amphisporangiate flowers. From these two types of flowers in the primitive angiosperms, the similar types of flowers, as we now find them in both monocotyledons and dicotyledons, may very well have directly arisen.

**Fertilization in Angiosperms.**—The peculiar position of the ovules of the angiosperms, protected within the ovary, involves special adaptations for insuring fertilization. Instead of the pollen coming into contact directly with the ovule, as it does in the Gymnosperms, it falls upon the variously modified upper portion of the pistil, the stigma (Fig. 16, A). This is specially fitted to retain the pollen and to facilitate its germination, but the germination of the pollen itself is very similar to that of the gymnosperms. After germination the pollen-tube must traverse the whole length of the pistil before it finally reaches the ovules. The intermediate portion of the pistil, or "style," is usually cylindrical in form, and the central tissue is especially modified so as to form a special conducting tissue which nourishes the rapidly growing pollen-

tube, as it pushes its way through this conducting tissue until it finally reaches the opening of the ovule, which it enters and fertilizes the egg in much the same way as we have already described for the gymnosperms. The highly modified structures of the carpels, so different from the open leaf-like ones of most gymnosperms, is one of the most striking characters of the angiospermous flower.

The effect of fertilization is the development of the embryo from the egg and the hardening of the outer tissues of the ovule, which now becomes a seed, resembling very closely the seed of the gymnosperms. A marked difference in the seed may be noted, however. The "endosperm," or gametophyte tissue which surrounds the embryo, and which in the gymnosperms is developed before fertilization, in the angiosperm arises subsequent to fertilization, and is the result of the division of the endosperm-nucleus, which is formed by the fusion of the two polar nuclei (Fig. 16, C, *p*). The latter may also sometimes fuse with one of the male nuclei from the pollen-tube. The homologies existing between the endosperm of the gymnosperms and the angiosperms are not, therefore, entirely clear. It has even been claimed that the endosperm of the angiosperms is rather in the nature of an embryo than part of the gametophyte, but we are inclined to the older view that it really belongs to the gametophyte as it does in the gymnosperms, and that the nuclear fusion which

precedes the formation of the endosperm is not to be regarded as a real fertilization.

**The Fruit.**—The effect of fertilization extends beyond the ovule itself, and the carpels within which the developing seed are enclosed are also stimulated into growth as the result of pollination, and at maturity enclose the ripened seed within a "fruit." It is probable that the development of the fruit, evidently a highly important means for protecting the seed, has been one of the factors in the success of the angiosperms in their struggle for existence. The variety of fruits is almost as great as that of flowers, and it is quite as evident in many cases that the modifications of the fruit are associated with animals, which play an important part in the distribution of the seeds of the angiosperms. Some of the modifications of fruits which are pretty certainly concerned with their distribution through animal agencies, are the development of edible pulp, either from the carpels themselves or from neighboring tissue, and the development of grappling organs, hooks, or spines, or occasionally an adhesive pulp, as in the fruit of the mistletoe. Many fruits and seeds are especially adapted for distribution by the wind, as for example the wind-borne fruits and seeds of the willow, catalpa, dandelion, and maple. There is no doubt that these many successful methods of fruit distribution were also important factors in establishing the ascendancy of the angiosperms.

## MONOCOTYLEDONS AND DICOTYLEDONS

A survey of the multitude of angiosperms which everywhere abound shows two pretty well-marked series of forms. One series may be represented by a tulip or daffodil, herbaceous plants having smooth, elongated leaves with inconspicuous, unbranched, parallel veins, and flowers with the parts in sets of three, the two outer sets of leaves being alike. If the seedling plant is examined, it will be found to possess a single seed-leaf or "cotyledon"; hence these plants are called "Monocotyledons."

Mustard may be taken as a type of the second series. The seedling shows two opposite cotyledons; hence the name "Dicotyledon" applied to the series. The young plant increases rapidly in size, and an examination of the stem structure shows that the woody bundles of the stem continue to increase in size by the addition of new tissue derived from a layer of permanently growing tissue, or cambium, which results in a secondary thickening of the stem. This in the woody-stemmed shrubs and trees exhibits annual growth rings like those in the trunk of a pine or other coniferous tree. No monocotyledons show this type of secondary growth in thickness.

The leaves in the mustard are more or less deeply divided or cut, and their veins are much branched and more or less united into an elaborate network. The flowers have the parts in fours, although the

outer set of stamens and the carpels are reduced to two. The outer floral leaves are differentiated into a calyx or outer envelope, and a corolla, the inner highly colored set of floral leaves.

When we try to determine the relative rank of these two series, we are met by much the same difficulties that we encounter in attempting to trace the connection of the angiosperms as a whole with the gymnosperms or pteridophytes. So far as the geological record goes, the two types seem to have developed almost simultaneously. It was formerly supposed that certain Paleozoic and early Mesozoic impressions of leaves belonged to monocotyledons, and that the greater antiquity of the latter was established; but much doubt has been thrown upon the nature of these fossils, and they are now generally considered to be remains either of Cordaitales or cycads. As the great majority of living monocotyledons are herbaceous plants, often of very delicate texture, it is by no means unlikely that they may have existed earlier than is indicated by the fossil record, and the same may be said of some of the lower types of dicotyledons, although in the latter group, many of what are regarded as primitive types are trees, like the willow, poplar, and plane, and these are among the earliest fossil angiosperms that we know.

**Fossil Angiosperms.**—There seems to be no reasonable doubt (see Zeiller: “*Éléments de Paléobotanique*,” 1900) that remains of both monocoty-

ledons and dicotyledons occur in the Infra-Cretaceous rocks; but the evidence of the occurrence of either group in earlier formations is extremely doubtful. If we try to determine the question from a study of the living forms, the matter is equally difficult. Among both monocotyledons and dicotyledons, flowers of equal simplicity are met with. Such monocotyledons as the arums, pond-weeds, or screw-pines may be compared to such apetalous dicotyledons as the peppers or willows; while the primitive type of amphisporangiate flowers with its indefinitely multiplied free parts, like the magnolia and buttercup, occurs also in the water-plantain and some other low monocotyledons.

There is no doubt that as a whole the monocotyledons are simpler than the dicotyledons, but the question then arises, whether this greater simplicity is not in many cases secondary, the result of reduction. The same difficulty is again met with in comparing the embryo, whose character gives name to the two series. While most dicotyledons, as their name implies, have embryos with two cotyledons, there are some in which but one is present, and the question whether the monocotyledonous or dicotyledonous condition is more ancient still remains open. It is quite conceivable that the two divisions, as usually recognized, do not necessarily represent two closed developmental series, and whether we consider monocotyledon or dicotyledon as the more primitive type,

it is not impossible that from this primitive group more than one line leading to the other may have arisen.

**Recent Theories as to Origin of Angiosperms.—**

Several recent writers have argued for the derivation of all the angiosperms from types allied to some of the Mesozoic Cycadales, in which the sporophylls are arranged very much as they are in the living magnolia. It is also argued that the gymnosperms and pteridophytes show, for the most part, structures approximating the dicotyledonous type, rather than that of the monocotyledons, and, moreover, that the embryo in the gymnosperms is usually dicotyledonous. From this hypothetical dicotyledonous ancestral form, with presumably woody stem and amphisporangiate flowers, types with the simpler monosporangiate flowers, and herbaceous habit, would be derived by reduction.

There may, however, be said, on the other side, that most of the gymnosperms and pteridosperms are monosporangiate, and primitively so. Moreover, the embryo of the ferns, and the same is true of the peculiar aquatic heterosporous pteridophyte *Isoetes*, which in many ways is strikingly similar in habit to the monocotyledons, is monocotyledonous; so it will be seen that something may be said for the assumption that the primitive angiosperms were monocotyledons and monosporangiate. It seems to the writer that the evidence available indicates that the two types of flower—the monosporangiate type,

such as occurs in the screw-pines and willows, and the amphisporangiate type of the magnolia and water-plantain, may be equally primitive, and not derived one from the other.

Whether these two types first arose in monocotyledons or dicotyledons must remain for the present an open question. It is quite likely that the primitive angiosperms were not clearly divided into monocotyledons and dicotyledons as they are now understood. From this primitive stock presumably more than two series arose, and these may have started with either type of flower. Thus at present some of the so-called Ranales, i.e., buttercups, water-lilies, etc., are dicotyledonous forms which are almost certainly directly related to such monocotyledonous types as the water-plantain and pond-weeds; while we believe a similar relationship exists between the monocotyledonous arums and the dicotyledonous peppers. Thus, while it is reasonably certain that all of the angiosperms belong to a common stock, it by no means follows that there may not have been developed from this more than one line both of monocotyledons and dicotyledons.

### MONOCOTYLEDONS

Whether or not the monocotyledons are more primitive than the dicotyledons, there is no question that as a class they are decidedly simpler, both in their external form and in their tissues. As their

name indicates, the embryo is provided with a single primary leaf, or cotyledon, and is thus easily distinguished from that of most dicotyledons, some species of which, however, have monocotyledonous embryos.

As a rule, the monocotyledons are herbaceous plants, very often having their leafy shoots arising from special permanent underground structures, root-stocks, bulbs, tubers, etc., and this "geophilous," or underground, habit of the stem has been assumed to be an adaptation which accounts to some extent for the reduced character of many monocotyledons, but this is an hypothesis which requires further demonstration before it can be accepted without question. The leaves, as a rule, are simple, smooth-margined, with parallel venation, but many arums and some lilies have net-veined leaves, like the dicotyledons. Very few of the monocotyledons are trees, the most marked exceptions being the palms and some screw-pines, although even among the lilies there are certain genera, like *Yucca* and *Dracæna*, which may attain the dimensions of small trees. No monocotyledon, however, shows the type of secondary thickening of the trunk, which is so common in dicotyledons, and in the few cases where there is a secondary thickening of stem it is of quite a different character.

The absence of cambium from the woody bundles of the stem is a constant feature in mono-

cotyledons, but it has been claimed that traces of such thickening tissues have been found in the seedlings of many monocotyledons, indicating that its absence in the woody bundles of the mature plant is a secondary condition. While the monocotyledons are as a rule less conspicuous than the dicotyledons in the flora of most regions, there are certain types which are gregarious and predominate over large areas. This is conspicuously true of the grasses in open prairie country; and in swampy districts, rushes, sedges, etc., may be found to be the principal constituents of the vegetation, and under these conditions are evidently quite able to hold their own in competition with the usually more aggressive dicotyledons.

**Monocotyledonous Flowers.**—The flowers of the Monocotyledons, as we have already seen, belong to the two principal types, apetalous and petaloideous. Of the former, some of the types cannot readily be explained as reductions from petaloideous flowers, and they are in all probability really primitive types. Such, for example, are the flowers of the cattail rushes, the bur-reeds, and the screw-pines. The two last, in addition to the simple type of flowers, show marked indications of the more primitive condition of the gametophyte, which is much better developed than in most angiosperms. The arums and palms are also probably old types, not reduced from petaloideous forms, but as in these two families both hermaphrodite and diclinous flow-

ers occur, it is a question which of these two types is the older.

The petaloideous monocotyledons constitute the second category, in most of which the floral envelopes are conspicuous, and these include some of the most beautiful and highly specialized of all flowers. The simplest types are seen in the lilies, e.g., tulip, hyacinth, trillium, etc. They have the characteristic three-fold arrangement of the floral organs with all the parts separate except the three united carpels; but the leaves of the floral envelope may be more or less united, as in the hyacinth or lily-of-the-valley. This appears to be the central type from which have radiated several lines of development, resulting in flowers differing a good deal from the primitive lily type.

The deviations from the primitive type are two-fold. First there is a reduction in the number of stamens, and second, a more or less complete fusion of certain parts of the flower. The simplest case is seen in the *Amaryllis* family, of which the narcissus and snowdrop are common examples. In these flowers the base of the floral envelope, and probably to some extent the floral axis, are fused with the lower parts of the carpels, so that there is formed an "inferior" ovary. Otherwise, the flowers are like those of the lily. In all of the higher types of monocotyledonous flowers there is an inferior ovary. In the *Iris* family there is a reduction of stamens to three, and a strong tendency to replace the radial symmetry

of the flower by a bilateral symmetry, as in *Gladiolus* (Fig. 17, C). In the *Canna* only one stamen is perfect, and the others are modified into petal-



FIG. 17

**Types of Monocotyledonous Flowers.**

A—Pistillate flower of Bur reed (*Sparganium*).

B—Staminate flower of Arrow-head (*Sagittaria*).

C—Flower of *Gladiolus*. The flower is "Zygomorphic," the stamens reduced to three, and there is an "interior" ovary, *o*.

like organs, while the flower is strongly zygomorphic, i.e., is bilaterally symmetrical.

It is among the orchids, however, that we find the most highly specialized type of flowers among the monocotyledons. This great family, the largest one among the monocotyledons, has the stamens generally reduced to a single one,

which is more or less completely fused with the upper part of the carpel, forming a peculiar structure known as the column, which distinguishes the flowers of the orchids (Fig. 22, B). The flowers are strongly zygomorphic, and like most highly specialized flowers they are, as a rule, quite dependent upon insect aid for pollination. The orchids, which constitute the second largest family of flowering plants, show the highest degree of specialization found among the monocotyledons, and also exhibit remarkable plasticity, as they grow under a great variety of conditions. There are many epiphytic orchids, or "air plants," and a good many which have lost their chlorophyll and become saprophytic, living upon the decayed organic matter in leaf mold. The orchids, however, do not as a rule seem to be capable of adapting themselves readily to new conditions, and never seem able to compete successfully with the more aggressive plant types when they are removed from their usual environment. They give the impression of a group of plants in the process of evolution, making experiments in various directions, and developing a great variety of types, most of which, however, are more or less pronounced failures.

### DICOTYLEDONS

**Dicotyledons the Highest of All Plants.**—The angiosperms, in the dicotyledons, reach their most

perfect expression, and these may be considered to represent the highest achievement of the plant type. Both in their superior numbers and adaptability they show themselves to be, as a class, better fitted to existing conditions than do any other class of plants, and probably among them are the most recent plant types that have been evolved. They include plants adapted to practically all conditions of life, and in one respect only are they surpassed by the monocotyledons, namely in their adaptation to a strictly aquatic condition. The number of truly aquatic types is relatively small, although some of them, like the bladder-weeds, are especially adapted to aquatic life, and one peculiar group, the Podostemonaceæ, have been so modified as to look more like algæ than flowering plants. No forms are known which live in sea water, the nearest approach to this being certain salt-marsh plants, and the mangroves.

They may be considered, as a class, to be more decidedly terrestrial in habit than are the monocotyledons. From tiny herbs, living but a few weeks, to giant trees, living as many centuries, dicotyledons are everywhere encountered, and usually in greater numbers, both of individuals and species, than are the monocotyledons. Except for certain coniferous trees, the dicotyledons make up the forests of temperate climates; and with the exception of the palms, they may be said also to constitute the great bulk of the tropical forests. The tendency

to develop permanent woody stems is a marked character of the class, and this is due to the development of cambium, or permanent growing tissue, in the woody bundles of the stem, very much as in the conifers, and in the stems of some ancient pteridophytes. This gives them the advantage of a permanent growth of the stems, which do not have to be formed anew each year, as is so commonly the case with monocotyledons.

With the greater diversity of the stem structure goes an equally diversified leaf type. The leaves may be either simple or divided, and in many cases elaborately dissected in a variety of ways. The great adaptability of the dicotyledonous type is well shown by the history of various weeds. While some of the weeds are monocotyledons, the grasses ranking first in this category, many more weeds are dicotyledons, which often have been brought from remote lands but have very quickly made themselves at home, not infrequently driving out the native flora. Climbing plants, carnivorous plants, epiphytes, parasites, and aquatics are some of the types that have been evolved among the dicotyledons.

**Flowers of Dicotyledons.**—The flowers of the dicotyledons (Fig. 18) are far too various in their structure to permit of anything more than the briefest sketch of their more salient features. Like the monocotyledons there are two main categories, apetalous and petaloideous forms. A number of very

characteristic orders of no very close affinity, however, are often grouped under the head of *Apetalæ*. Some of these, both upon structural grounds and

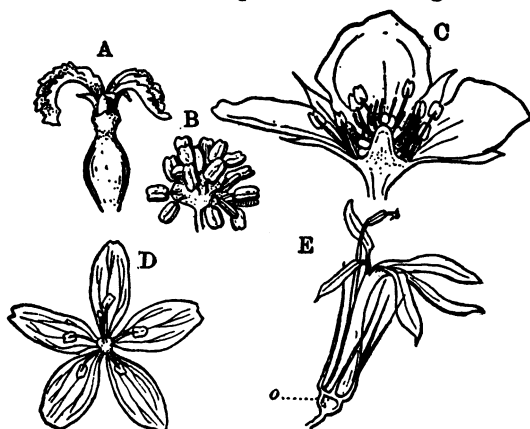


FIG. 18

Types of Dicotyledonous Flowers.

A—Pistillate flowers of Walnut.

B—Staminate flower of Poplar.

C—Section of apocarpous flower of Strawberry.

D—Choripetalous flower of Spring-beauty (*Claytonia*).

E—Sympetalous, zygomorphic flower of Cardinal flower (*Lobelia*).

from geological evidence, are evidently ancient types, and there is no good reason to consider them as reduced from petaloideous forms. Such, for example, are the willows, poplars, oaks, and walnuts. These all have diclinous flowers, and it is difficult to say from what amphisporangiate forms they could possibly have been derived. The flower consists either of stamens or carpels, and the floral

envelope, if present at all, is of the simplest character (Fig. 18, A, B).

The petaloideous forms show great variety, and it is not easy to reduce them all to one series. The type of the flower found in the buttercup or magnolia is regarded as primitive, but it is difficult to connect these forms with such apetalous flowers as those of the poplar or oak, for example. There are other simple petaloideous types, such, for example, as the pinks, portulacas, etc., which are quite different from such apocarpous types as the buttercup or water-lily. These lower petaloideous types have been called Choripetalæ, and have the petals entirely separate. The number of carpels and stamens may be quite indefinite or they may be of definite number.

The specialization of the flower in the dicotyledons has proceeded very much in the same way as among the monocotyledons, and affords another example of parallel development. There is first an indefinite number of entirely separate parts, then a reduction in the number of stamens and carpels, and a tendency toward a coherence of certain parts, resulting in a more or less tubular flower, with inferior ovary and a reduced number of stamens. Where the petals are grown together the flower is said to be "sympetalous," and the Sympetalæ, which include all such flowers, are considered by botanists to be the most highly specialized of the dicotyledons (Fig. 18, E; Fig. 19, F).

Among the Choripetalæ there are much greater differences of structure than among the Sympetalæ, which are reducible to a comparatively small number of types, although in point of numbers they probably surpass the Choripetalæ. It is among these highly specialized Sympetalæ that we meet with the most successful types, these being the dominant dicotyledons, especially in the tropics.

The largest family of angiosperms and the one which, on the whole, seems to have succeeded best in the struggle for life, is the Compositæ. The universal distribution of Compositæ and the aggressive character of many of them are sufficient proofs of the efficiency of this type. This superiority seems to be more or less due to their extraordinarily perfect devices for the transportation of their seeds. The numerous wind-borne seeds of the dandelion and thistles, the tenacious burs of the bur-marigold and burdock, together with the robust constitution of the plants themselves, have given these weeds an enormous advantage in the struggle for existence; and we see them scattered over vast tracts of country, taking possession of the vacant ground almost to the exclusion of the plants originally inhabiting them.

**Evolution of the Flower in Monocotyledons and Dicotyledons Much Alike.**—The evolution of the flower has followed very much the same course in monocotyledons and dicotyledons, and illustrates once more the remarkable similarity that may result

from response to similar conditions in independent developmental lines (Fig. 19). This would seem to be an excellent illustration of determinate variation

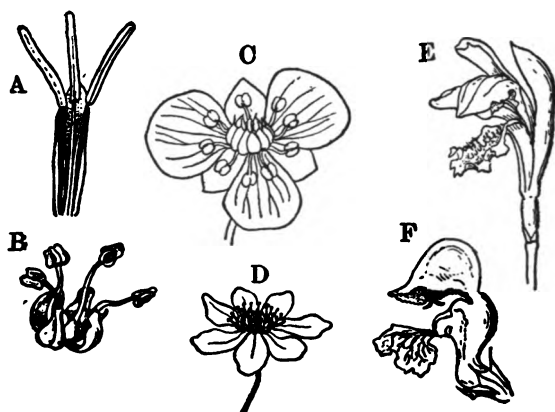


FIG. 19

Parallelism in the evolution of the flower in Monocotyledons (upper row) and Dicotyledons (lower row).

A—Apetalous flower of a Sedge (*Carex*).

B—Apetalous flower of a Mulberry (*Morus*).

C—Apocarpous flower of Water-plantain (*Alisma*).

D—Apocarpous flower of Rue-Anemone (*Thalictrum*).

E—Zygomorphic sympetalous flower of an Orchid (*Arethusa*).

F—Zygomorphic sympetalous flower of Dead-nettle (*Lamium*).

(Fig. C, after Britton & Brown.)

in several lines starting from a common stock and resulting in very similar structures at the end of these diverging lines of development. In both of the great divisions of the angiosperms, the lower types

of flowers, whether monosporangiate or amphisporangiate, have all the parts entirely separate and often indeterminate in number. These simple types are often inconspicuous and are probably all capable of self-pollination, supposing that they are amphisporangiate. Where the flowers are diclinous, and often when they are amphisporangiate, as in most grasses, the distribution of the pollen is almost always effected by the wind. With the increase in specialization, the flower first assumes a definite number of parts, and there is a tendency towards cohesion of its parts, which is usually seen first in carpels. Such floral types as the lilies and mustards are examples of this. In the typical monocotyledonous flowers the carpels are equal in number to the other cycles of floral leaves, but in most of the dicotyledons the number of carpels is reduced. There are, however, numerous types among the simpler dicotyledons where the carpels are also equal in number to the other parts of the flower, and these are said to be "isocarpous." The geranium and flax may be cited as examples of such isocarpous flowers.

The cohesion of the floral parts increases with the specialization of the flower, and this may even extend to the stamens as well as the corolla. Thus in some of the Pea-family the stamens are grown together into a tube, and the same is seen in the mallows. The carpels in the greater number of angiosperms are grown more or less together and form

a "syncarpous," or compound pistil. The lower part of the pistil, or ovary, usually clearly shows the number of carpels of which it is composed either by being divided into chambers or having a corresponding number of placentæ, from which the ovules grow. The upper part of the floral axis is frequently extended into a tube at the bottom of which the ovary lies, and in very many flowers both Chori-petalæ and Sympetalæ, the lower portion of the tube may be completely fused with the ovary, and the latter is then said to be inferior, the other parts of the flower being "epigynous." Such epigynous flowers are considered to be more specialized than those in which the ovary is free. The iris, narcissus, canna, and the orchids are typical examples of epigynous monocotyledons, while the fuchsia and the Compositæ are illustrations of epigyny in the dicotyledons.

Sympetaly, or the union of the petals, is a common phenomenon in both the monocotyledons and dicotyledons. It reaches its extreme in such flowers as the morning-glories or the fox-glove, where the limits of the individual segments or petals are almost obliterated. Finally in the orchids there is an almost complete coalescence of the carpels and stamens, the latter being reduced in most cases to a single one.

**The Most Specialized Flowers are Zygomorphic.**—In the more primitive flower the parts are usually arranged radially, but in many flowers the sym-

metry is bilateral, the flower often being two-lipped, as in the sage and other "labiate" flowers (Fig. 19, E, F). This "zygomorphy" is frequently associated with a reduction in the number of stamens, as in the fox-glove or snap-dragon, where instead of the five stamens which would correspond to the number of petals, there are but four. Sometimes a rudiment of the fifth stamen is visible, as in the *Pentstemon*. Zygomorphy does not necessarily involve a reduction of the stamens, the sweet-pea, for instance, having ten stamens, or twice the number of the petals.

**Perfume and Color as Lures for Insects.**—The inconspicuous flowers of the *Apetalæ* are usually destitute of perfume, which is so marked in so many flowers. There seems no good reason to doubt that the presence of strong odors, agreeable or otherwise, is associated with the visits of insects which are attracted to the flower both for the sake of the pollen, which was probably their first object in visiting the flowers, and for the sake of the nectar which is secreted by many of them. The gay colors of the petals and sometimes of the other parts of the flowers, or inflorescence, e.g., the stamens in *Eucalyptus*, the sepals in the *Clematis*, or the accessory bracts in the arum, or dogwood, are usually also regarded as a means of attracting insects or birds.

There has been lately a tendency to minimize the importance of insects as the agents of cross-pollination, and the significance of the coloring of the flow-

ers in attracting these, and it is quite possible that the assumption of the keen power of discrimination of different colors and markings which has been attributed to insects has been exaggerated; but the evidence is overwhelming that there is a direct connection between the development of showy flowers, and cross-pollination through insect agency.

**Cross-pollination.**—While many showy flowers, when insect visits are prevented, pollinate themselves, there are very many in which cross-pollination is absolutely indispensable owing to mechanical contrivances by which self-pollination is rendered impossible. Some of these will be discussed more at length in a future chapter. Where specialization reaches its extreme, pollination may depend upon a single species of insect, as for instance, in certain orchids and species of *Yucca*.

**Insects as Agents in Pollination.**—One group of animals has played a very important rôle in the evolution of the flower of the angiosperms. These are the insects, the largest group of animals, bearing somewhat the same relation, in point of numbers, to the animal kingdom that the angiosperms do to plants. Vast numbers of insects are dependent upon plants for their existence, and many of the peculiar modifications of their structures are unquestionably correlated directly with the structures of angiospermous plants; and the modifications of the flowering plants and insects have presumably gone on side by side, each affecting the other. Thus the pe-

cular mouth-parts of the flower-haunting insects, like the bees and butterflies, unquestionably owe their existence to the peculiar structures of the flowers they visit, and the flowers become adapted to the associated structures of the insects. The enormously long proboscides of the big hawk-moths are only to be explained as organs especially fitted for probing the deep nectaries of certain flowers, and the pollen-receptacles of the bee must have been developed in connection with the habit of collecting pollen for food. It has often been claimed that the peculiar formation of many flowers is the direct reaction to stimuli, due to the irritation of special parts of the flower during the visits of insects. It may be said, however, that this view is not generally accepted.

**Birds as Agents in Pollination.**—Many flowers are adapted to fertilization by birds, which have become modified accordingly. The great American family of humming-birds, and the honey-suckers of the Old World, are the best-known types. These two groups of birds, although not at all related, show curiously similar characters in size, color, and form, and the flowers they frequent, both in shape and color, show a corresponding similarity. Bright red seems to be the favorite color of these much frequented flowers, and in America many vivid red flowers, like the trumpet-creeper, the scarlet balm, scarlet sage, trumpet honeysuckle, and many others may be mentioned as special favorites of

humming-birds; while in South Africa, the scarlet Aloes and coral trees (*Erythrina*) are particularly favored by the sun-birds.

Whatever other advantages may come from cross-pollination, increased variability is undoubtedly one result, and this may account in part for the rapid evolution of new forms among the angiosperms, and their enormous preponderance at the present time.

**Fruits of Angiosperms.**—The fruits of the angiosperms show a variety, which while not equal to that of the flowers, nevertheless is very great. The lower types have the fruit in the form of a dry capsule, which opens at maturity and scatters the seed, or sometimes it may be an indehiscent one-seeded fruit, like that of many grasses, or the buttercup. Such fruits have often to depend upon chance for their distribution of seeds, just as the lower floral types are dependent upon the wind for transporting their pollen. With the evolution of plants, however, many modifications of the fruit arose as the result of which the distribution of the seeds was facilitated. This distribution may be in some cases by means of water, but more commonly it is due to the wind, or the agency of animals. Of fruits adapted to water transport, the cocoanut is the classic example. The gigantic seed, enclosed in its thick water-proof covering, is eminently fitted for long immersion without suffering, and may be carried great distances by the ocean currents. Contrivances

for transportation through the agency of the wind are extremely numerous, but will have to be passed over here. As well as assisting in the pollination of flowers, animals are very important agents in transporting the fruits, which may be attractive to them as food, in which case the enclosed seeds are thrown aside and scattered, or are swallowed and pass through the body of the animal undigested, and are ejected in the excreta. Birds are especially important in this distribution of seeds, owing to their rapid flight and their long migrations, and doubtless many widespread species of plants owe their distribution mainly to bird agency. Other modifications associated with the distribution of seeds through animal agencies are the adhesive organs of seeds and fruits by which they cling to the coats of animals and are carried from place to place.

**Angiosperms Adapted to All Conditions of Life.**

—The many special modifications of the angiosperms, adaptations to all the varied conditions of life, can only be touched upon here, but later will be considered more at length. Among them there are plants fitted to almost every possible condition under which plants can grow at all. While reaching their most luxuriant development in the hothouse conditions of the equatorial lowlands, they can also grow at the very limits of vegetation in the polar regions, or upon alpine summits; under the fierce sun of the desert, or completely submerged

in the ocean. Struggling for light in the fierce competition in the tropical zones, climbing plants of many types have been evolved, and many epiphytes, or air plants, may be seen perched almost at the very tops of lofty trees. Some species, like the giant *Rafflesia*, are parasites of the most extreme type, and pass nearly their whole existence within the tissues of their host, exactly as a fungus does, and like the fungus they expand their reproductive parts in the air. A still larger number are more or less completely saprophytic, extracting their nourishment from the organic débris of the forests, much as the toadstools and other larger fungi do; but it may be stated that in order to do this they seem obliged to call in the assistance of a true fungus, with which they always seem to be associated. These are but a few of the manifold adaptations shown by this protean plant-type.

#### SUMMARY

While the early history of the angiosperms is wrapped in obscurity, the evidence at hand indicates that the first angiosperms probably appeared rather suddenly towards the end of the Mesozoic. Whether they arose from gymnosperms, possibly allied to cycads of the Mesozoic, or whether they were derived more directly from some fern-like ancestors, must for the present remain unanswered. The remarkable uniformity in their essential structures,

shown by all of the existing angiosperms, makes it almost certain that they are all derived from some common stock, or at any rate from a group of forms closely related to each other. Once established, the angiospermous type showed itself to be peculiarly adaptable, and it rapidly assumed a predominant position. Whence arose their extraordinary plasticity can only be conjectured. The type of fruit, with its complete protection of the seed until its maturity, may have been one of the important factors in establishing this superiority over the cycads with their exposed seeds, although it must be said that in the cycads the growing seed is generally more or less protected by the scales of the cone. But this will not explain the extremely plastic plant body which contrasts so strongly with the limitations of the plant-body in the gymnosperms.

It is possible that cross-pollination among the angiosperms developed very early, and that thus there was induced a greater degree of variability resulting in the appearance of many modifications which could be seized upon by natural selection, and thus tend to develop new types. Whatever may have been the reason, it is their extraordinary adaptability that is at the bottom of the remarkable success attained by the angiosperms. One very important phase of this is the utilization of animals for distribution of pollen and seeds. This is not absolutely confined to the angiosperms, as occasionally the spores of fungi are

distributed by insects, and *Welwitschia*, one of the gymnosperms, but possibly allied to the angiosperms, is supposed to be entomophilous. Most of the plants whose organs have been modified with reference to animal structures are angiosperms, and the extraordinary variety of flowers and fruits is doubtless due in a large measure to such adaptations.

Which is the older of the two main divisions of angiosperms must remain for the present in doubt. The geological record is very unsatisfactory on this point, and comparative morphology gives hardly any more certain answer. It is possible, at least, that the divisions into monocotyledons and dicotyledons is a somewhat artificial one; and it may be that from an indifferent primitive stock, angiosperms in all essential respects, a number of lines arose, some to become monocotyledons, others dicotyledons.

The question as to the nature of the primitive angiospermous flower is also not at all satisfactorily settled. While some of the diclinous floral types can be explained as reduced from hermaphrodite ones, it is by no means always the case, and we believe that some, at least, of these diclinous types, are really primitive. This implies that before monocotyledons and dicotyledons were established as such, both types of flowers had developed, and these in the further course of evolution were transferred to both monocotyledonous and dicotyledonous families.

Whatever may have been their origin, the extraordinary fitness of these plants to modern conditions is obvious, and they have taken possession of the land-areas of the whole world almost to the complete exclusion of other plant types. Only under exceptionally favorable conditions are the lower plant types able to hold their own in competition with the all-conquering angiosperms.

## CHAPTER VII

### ENVIRONMENT AND ADAPTATION

**W**HAT were the conditions prevailing upon the earth when the first organisms appeared, must remain purely conjectural. The earliest forms of life have left no recognizable traces, and the first unmistakable plant remains are so highly organized as to make it certain that these must have been preceded by a long series of simpler forms. As we have already indicated there is some reason to believe that the bacteria and blue-green algae more nearly approach the primordial plants than do any other living forms; but whether or not these were the progenitors of the higher plants is another question. The resistance of many of these organisms to very high temperatures and other conditions which are not favorable to the higher plants, suggest that the conditions of life during the earliest history of the plant kingdom were different from those existing at present, but of course we can only guess what these conditions were.

**The Higher Plants Derived from Algae.**—A study of the evolution of the higher plants makes it almost certain that these are descended from green

algæ, probably not very different from some of the existing fresh-water forms. The extraordinary persistence of the motile reproductive cells, found as high up as the lowest of the seed-plants, indicates that the ancestors of the modern land plants were algæ, whose pedigree can be traced back to free-swimming unicellular plants, resembling some of the existing Volvocales. These green "Monads" may be assumed to have abounded in the seas of the earlier geological epochs. It has been assumed that the water of the primordial seas was fresh or only weakly saline, and would, therefore, have been adapted to the existence of forms like the modern green algæ, which at present are mainly fresh-water species. With the increasing salinity of the ocean, many of these more primitive green algæ probably retreated to the smaller fresh-water bodies, where they have persisted, perhaps but little changed, from the remotest times; while in the more saline ocean water, the two groups of typical seaweeds, the red and brown algæ, have developed and taken the place of the primitive green forms, their peculiar characters becoming more and more pronounced with the increasing salinity and other changes of their environment.

**Uniform Conditions in Fresh Water.**—Except for differences of temperature the conditions of life in fresh water are very uniform, and it is not remarkable that the range of structure in the fresh-water algæ is relatively slight. The most primitive

of the unicellular Volvocales may be taken to represent the commencement of the series leading up to the higher plants. The earliest plants may be assumed to have been motile like the existing Volvocales, but the power of motion was probably early lost in the vegetative cells, this being associated with the power of photosynthesis, which does not make it necessary for the plant to move about for food.

So long as the plant is completely immersed no special organs are necessary for absorbing the water with the dissolved food constituents, these being taken in freely at all points of the surface. Moreover, such submerged plants are not subject to loss of water through evaporation, and therefore the superficial cells do not need to develop a cuticle.

### MARINE PLANTS

The relation of the seaweeds to the simpler and probably more ancient fresh-water algæ is largely a matter of speculation. The true brown algæ are hardly at all represented in fresh water, but there are a number of fresh-water organisms which may be remotely related to them. The development of large amounts of gelatinous or mucilaginous tissues which hold the water with great tenacity, and also absorb water very rapidly when the plants are wet by the rising tide, has already been referred to. Some of the large kelps may be exposed to the air for days before all of the moisture is lost from

their tough leathery fronds. This power of retaining water is exhibited in a lesser degree by some fresh-water algæ, especially those forms which live in the temperate regions and are only part of the time in the water.

Owing to their perfect adaptation to life in salt water, the brown and red algæ have found few competitors and may be said to dominate the flora of the sea. Whatever may be the reason, salt water seems to exercise a stimulus which induces a much more luxuriant vegetation, and as we have seen produces greater variation than does fresh water. Sea-weeds growing in pure sea water have been found to be more robust than the same species growing in brackish water, for instance near the mouths of streams. The common rock-weed (*Fucus vesiculosus*) and one of the red algæ, a species of *Poly-siphonia*, are examples.

**Marine Algæ.**—The red algæ are not so exclusively marine in their habit, and the lower members of the class show sufficient points of resemblance to the green algæ to make it possible that they may be offshoots of the latter. The conditions of life in the sea are very different from those in fresh water, perhaps the greatest difference being the marked salinity, and consequently greater density of sea water—a condition which has involved great changes in the structures of marine plants. The conditions in the sea are evidently conducive to great variability, and we find the seaweeds reaching a size

and complexity with which none of the fresh-water algæ can compare. This culminates in the giant kelps, whose great leafy shoots may be hundreds of feet in length and in their form suggest the higher land plants. That the increase of salinity seems to induce variation has been noted repeatedly. It has been observed that in adjacent areas, differing merely in their salinity, the less saline water is very much poorer in the number of species than the more saline water. While the brown and red algæ predominate in the sea, there are many green algæ found there also, and the latter are much less sensitive to changes in salinity of water than are the more highly specialized brown and red seaweeds, the latter of which are often quickly killed by slight changes in temperature and salinity. A good many species of both brown and red algæ show a certain amount of adaptability, and may adjust themselves to slightly saline, and even brackish water, as, for instance, near the mouths of rivers flowing into the sea.

**Marine Life Checks Sexual Reproduction.**—It may be safely assumed that the green seaweeds are probably immigrants from fresh water, which have become modified more or less by their changed environment. A striking peculiarity of all of the green seaweeds is the primitive condition of their reproductive parts, although many of them are plants of considerable complexity. No green seaweeds are known in which the gametes are perfectly

differentiated into eggs and spermatozoids. It may be that life in salt water may tend to check the evolution of the sexual system. It is true that in one group of brown algæ, the Fucaceæ, sexuality



FIG. 20

The Sea-palm (*Postelsia*), an alga adapted to life in the surf; the long flexible stem is firmly anchored to the rocks by a powerful holdfast, a root-like grappling organ.

is well developed, but in a very much larger number the sexual elements are very simple, being motile gametes, or the plant may be entirely sexless. In the largest of all of the brown algæ, the giant

kelps, no sexual reproduction has been demonstrated.

It is pretty clear that the lack of resting spores in the marine algæ is correlated with their absolute freedom from danger of drying up. It may be that the advantages of the numerous quickly germinating reproductive cells, such as the zoöspores and isogametes of most of the brown and green seaweeds, or the spores of the red algæ, have been so great that they have remained in their present state of development as the result of natural selection.

**Surf Algæ.**—Certain very obvious adaptations to a marine environment are the tough and flexible tissues found in the larger kelps and red seaweeds which are exposed to violent surf. This is very beautifully shown in the great kelps that abound along the rocky coasts of Pacific North America. Some of them, like the sea-palm (*Postelsia*) (Fig. 20), cling to the most exposed rocks, where they are constantly battered by the full force of the heavy waves that dash against the shore. These kelps, with their elastic leathery fronds and powerful holdfasts, grip the rocks securely and withstand uninjured the heaviest pounding of the surf.

## TERRESTRIAL PLANTS

The conditions of life in water are much less variable than on land. Temperature changes are less extreme and rapid, and of course the amount of wa-

ter supplied to the plant is constant, and provisions for the conduction of water and for its conservation are unnecessary; hence the absence of these in such submersed aquatics as most of the algæ. However, where the plant reaches a great size, as in the kelps, conducting tissues for the transport of assimilated material may be very perfectly developed. While variations of light to which algæ are exposed are somewhat less extreme than is the case in land plants, it is evident that the question of light has been one of the most important factors in the modifications of the algal types, since the varying depth of the water, as well as the shade of the rocks and larger algæ, must cause great differences in the intensity of the light, with a corresponding variation in the plants adapted to these lights of different intensity.

As we have endeavored to show, the first land plants probably arose from forms allied to some of the existing fresh-water algæ, which became adapted to life on land by the development of roots for water absorption, and more or less perfect protection of the exposed tissues against undue loss of water. This is secured either by the development of mucilaginous or gelatinous envelopes, or by the cuticularization of the exposed cell walls. This primitive type of land plant probably culminated in the higher mosses, but it never became quite perfectly adjusted to terrestrial conditions, since the simple hair-like roots could only suffice

for a plant of moderate size, and the mechanical, or supporting tissues, which enable the terrestrial plants to overcome the force of gravity, are indifferently developed in the mosses. It has also been pointed out that, having exhausted the possibilities of an aquatic gametophyte, after its translation to land, nature seems to have taken up the neutral generation or sporophyte as a more promising subject for further experiments in the development of a truly terrestrial plant type. The sporophyte, being originally an adaptation to terrestrial conditions, seems to have a much greater potentiality for development as a land plant, and once thoroughly established as such, superseded the algæ and mosses as the prevailing type of land vegetation. The ferns or Pteridophytes are the first of these typical terrestrial plants. Their preëminence is due to the development of true roots capable of indefinite growth to correspond to the great development of the rest of the plant-body, which in these plants assumes a size and variety far surpassing anything attained by the lower plants. The sporophyte has shown itself to be extraordinarily adaptable, and has been able to establish itself under very different conditions of heat, light, and moisture. The elaborate root system, with the development of very perfect water conducting tissues, provides for rapid absorption and transport of water within the plant, and the outer tissues are effectively protected against undue loss of water by transpiration.

On the basis of their relation to water, three categories of plants are recognized: Hydrophytes or aquatics, Mesophytes or plants in which there is a normal supply of water but which are not true aquatics, and Xerophytes in which the need of conservation of water is more or less acute. Of course these groups are not absolutely separate from each other, and may be further subdivided.

### AQUATICS

Aside from the algæ, nearly all of which are true aquatics, there are a good many flowering plants and a few mosses and ferns, which are also to a greater or less degree genuine water plants. How far these forms are secondary, that is, are derived from originally terrestrial types, is not always easy to decide; but in many cases it is perfectly clear that they are modified descendants of terrestrial forms. These aquatics may be completely immersed, as in some of the pond-weeds and some of the sea-plants, like the eel-grass (*Zostera*); or they may be floating plants, like the little water-fern (*Azolla*), or the duck-weed (*Lemna*), etc., or they may be rooted below the surface of the water with floating leaves and flowers, like the water-lilies, or finally they may stand above the surface like the reeds, cattail-rushes, etc.

**Land and Water Plants Compared.**—Compared with the related land plants, these aquatics show

various modifications. Where the plant is completely submersed, the exterior tissues are quite destitute of a cuticle, and the stomata are entirely absent; but if any parts emerge above the water, such for instance as the upper surface of the water-lily leaf or the aerial leaves of the arrow-head, the epidermis shows the usual cuticle and stomata. Submersed leaves are generally either narrow or finely dissected, and the contrast between the submersed and aerial leaves of the same species is often very striking. Thus in the water-shield (*Cabomba*), and some species of water crowfoot, the aerial leaves are quite entire, or only slightly lobed, while the submersed leaves are finely divided into very narrow segments. How far the peculiar form of submersed leaves is directly due to the physical properties of the surrounding medium, and how much is to be attributed to adaptation to light and food conditions, has not been satisfactorily demonstrated. The more direct exposure to light and to the action of  $\text{CO}_2$  and free oxygen dissolved in the water, are probably important factors concerned with the form of these submersed leaves.

Comparatively few woody plants are aquatics, and where they have roots completely submerged they may show some interesting modifications, usually associated with the aëration of the roots. The curious growths from the roots of the southern cypress, known as "cypress-knees," and the aerial roots of the mangrove, are undoubtedly aërating organs.

The hydrophytes are sometimes characterized by the poor development of roots, which may actually be absent in some of them. Most of the hydrophytes are herbaceous plants, and the stems and leaf stalks are provided with very large air spaces.

## MESOPHYTES

Where plants are provided with an adequate but not excessive amount of water, they develop a perfect root-system, and an ample expanse of green tissue, either in the form of a flat thallus, or, in the higher plants, of leaves of various kinds. The size of the leaf is to a certain extent dependent upon the intensity of light and upon the amount of moisture, the two often being in inverse ratio. Other things being equal, transpiration is less active in the shade than in the full light, and shade plants normally exhibit a much larger leaf surface than those exposed to full sunlight. The difference is very evident in plants of the same species, or even in the same individual, and can be readily enough demonstrated. If the light is completely excluded, or is too weak for photosynthesis, there usually is a degeneration of the leaf lamina, which may be almost completely suppressed, a fact familiarly demonstrated by the blanched and shrunken leaves of a plant sprouted in the dark.

**Types of Leaves in Mesophytes.**—The increase in the extent of the leaf surface may be effected in

various ways. Some plants develop very many small leaves, others a few very large ones, and the latter may be entire as in the banana and many arums, or it may be very much divided as in some of the tree-ferns. Mesophytes predominate in the moister temperate regions and in the shaded forests of the tropics. With increasing moisture they approximate the hydrophytic type, and as the moisture decreases they assume more xerophytic characters.

### XEROPHYTES

The term "xerophyte" has been applied to those plants which exhibit more or less evident characters adapting them to growth with a limited water supply. As the amount of water is diminished in the normally mesophytic plant, it becomes dwarfed and the leaves are very much smaller, and at the same time there is a thickening of the leaves, and often greater hairiness. With the reduced leaf surface there is naturally a correspondingly diminished transpiration of water.

**Xerophytes Not Always Confined to Dry Regions.**—While most mesophytes are able to adapt themselves to a greater or less reduction in the water supply, there are many plants which normally grow in regions where they can receive only a very limited amount of water, and it is among these natural xerophytes that the most remarkable adaptations for economizing water are found. Xerophytes are

by no means confined to very dry regions, but may be found almost everywhere, even in regions of heavy rainfall. The character of the soil and the exposure may be such as to allow most of the water that falls to escape, and plants growing under such conditions must provide for this. Thus a plant growing on a steep gravelly hillside, or in the crevice of a rocky cliff, can use only a very small part of the rain that falls upon it, and consequently such plants will show a more or less pronounced xerophytic habit.

**Desert Plants.**—Of course it is in the more arid parts of the world that the xerophytes abound, and it is these desert plants that offer the most striking examples of xerophytic adaptation. The simplest method of checking the loss of water is by reducing the number and size of the leaves, and increasing the thickness of the epidermis. A plant growing on the dry hillside, contrasted with the same species in the moist valley below, will show this very clearly. In the more pronounced xerophytes the leaves may be entirely lost, as in the Spanish broom or in many cacti and some euphorbias. In such xerophytes the photosynthetic function is taken over by the superficial tissues of the stem.

This desert vegetation is very strikingly developed in the hot, arid regions of Northern Mexico, and the adjacent deserts of Southern California and Arizona. Among the most striking xerophytes of this region are the innumerable cacti, some like the

giant cactus, or Suwarro (*Cereus giganteus*), having almost tree-like proportions, and showing a maximum reduction of the evaporation surface, and extraordinary capacity for water storage. The extensively branched roots run close to the surface of the ground, where they quickly absorb the rain and convey it to the great pillar-shaped stem, where it is stored away deep in the sappy tissues of the pith.

The century plant (*Agave*), unlike the cacti, has its leaves highly developed, but these are very thick and fleshy, and protected by an impervious covering so that they are quite as efficient water-storage organs as the fleshy, leafless stems of the cacti.

Another remarkable plant (*Fouquieria*) of this same region is familiar to every observant traveler through Southern Arizona. This curious shrub, known locally as "Fish-pole Cactus," or "Ocotilla," is a bush consisting of a bundle of slender stems, sometimes tipped with a cluster of scarlet flowers, nearly or quite unbranched, and usually quite bare of leaves. Periodically, however, at the seasons when the brief showers of midsummer or midwinter fall, the bare stems clothe themselves with delicate little leaves, quite out of keeping with the desert environment, and these quickly wither with the cessation of the rains.

Sometimes the leaf becomes reduced so that the normal blade disappears, and a flattened leaf stalk takes its place. These "phyllodia" are especially perfect in some of the Australian acacias, often

grown for ornament, and their real nature can be seen by tracing the development of the leaves in the seedling, which at first always show a feathery lamina, which is gradually reduced in the later leaves, until it quite disappears, and nothing is left but a flattened leaf stalk. When these normally xerophytic plants are abundantly watered, it is quite common to find the leaves reverting to the feathery form on the more vigorous young shoots. In other cases like the prickly pear and the greenhouse "smilax" the leaf-like organs are really flattened branches.

**Water Storage.**—The storage of water is also an important function in xerophytic plants, and there are many types of storage organs. The root system is also modified with reference to the water supply and to the character of the aerial parts. In desert plants the roots may be very long and capable of reaching down to the deep-seated layer of water in the soil, or as has recently been shown by Cannon in his studies on the roots of desert plants, the root system may be very shallow, spreading extensively near the surface of the ground, where advantage may be taken of brief showers which wet only the superficial layers of the soil, and quickly evaporate. The water is promptly absorbed and conveyed to the aerial parts of the plant and there stored away for future use. The great cacti of the hot, arid regions of the Southwest are very striking examples of this xerophytic type.

Many xerophytes, like the cacti and century-plant, have fleshy stems or leaves with impervious outer tissues, which prevent loss of water, while the inner tissues are often mucilaginous and very retentive of the moisture which is stored up in great amounts. Such fleshy plants can be uprooted and exposed for weeks to the hot sun before all their moisture is lost.

**Bulbous Plants.**—Another xerophytic type is seen in the bulbous and tuberous plants, which are characteristic of many semi-arid regions like California, the shores of the Mediterranean, and the Cape region of South Africa. These bulbs or tubers may be exposed to drying up without losing their vitality, and will be found to retain a large amount of water for a long period. When proper conditions arise for their growth, the leaves and flowers are rapidly developed at the expense of the moisture and food stored up in the bulb, and after the seeds have matured, they wither away, leaving only the subterranean portions alive. Many familiar garden flowers are of this type, most of them coming from regions with a more or less pronounced dry season. California is very rich in bulbous plants, and many of these, like the beautiful Mariposa-lily (*Calochortus*), are among the most charming of our wild flowers.

**Halophytes.**—Resembling in many respects the true xerophytes, are the Halophytes, or salt-marsh plants. Although they grow where there seems to

be an abundance of moisture, these plants take up a relatively small amount, as the excess of salt dissolved in the water is not favorable for their growth. Hence these plants show the fleshy habit characteristic of xerophytes. Plants growing along the seashore often show this same fleshy texture. Examples of these strand plants are the ice-plants (*Mesembryanthemum*), sand verbena (*Abronia*), and sea-rocket (*Cakile*).

## LIGHT

### **Modifications Associated with Photosynthesis.—**

As photosynthesis is the most important of the nutritive processes of the plant, it is not surprising that some of the most striking modifications of the plant-body are obviously associated with chlorophyll work. In the cells of all of the algæ there are present definite organized structures, chromatophores, which are the essential photosynthetic organs, and the form and position of these is to a great extent correlated with the direction and the intensity of the light rays. In the lowest forms there is usually a single large chromatophore which may assume a very complicated form, as in some of the pond-scums (*Spirogyra*) or the desmids; or there may be two or more large chromatophores, which are often more or less divided, possibly a contrivance for increasing their efficiency. Only a relatively small number of the green algæ, e.g.,

Siphonæ and Characæ, have many small chromatophores like those of the higher plants.

The prevalence of the small chromatophores in the more highly specialized red and brown algæ, as well as in the higher land plants, would indicate that the numerous small chromatophores are probably more efficient than the single large chromatophore of the lower types. Aside from the modifications of the individual chromatophores, the character and arrangement of the cells containing them may safely be assumed to be related to light exposure. In the larger and more massive seaweeds, the chromatophores are mainly developed in the superficial cells, where they are best exposed to the light, and in the more delicate algæ the assimilative cells may be spread out in thin leaf-like plates, exposing a large area to the light, and sometimes the same result is obtained by the development of dense tufts of fine branches composed of single rows of small cells, which are thus exposed on all sides.

Among the red and brown seaweeds, secondary pigments are developed, but there has been much discussion as to their composition and as to the rôle they play in the plants' economy. The brown pigments of the kelps are pretty generally recognized as protective, screening the chlorophyll from too strong illumination. The brown algæ very commonly grow close to the surface of the water or actually floating upon it, or they may be completely exposed by the ebbing tide. Some of them grow

in deeper water, but it has been suggested that those living in deep water represent a secondary adaptation which has not caused the loss of the pigment, which, however, is no longer essential.

The case of the red algæ seems to be somewhat different. They are, as a rule, shade-loving plants, and grow either in deep water or in the shade of other large algæ or of rocks. It has been assumed that the red pigments of these forms enable them to absorb certain light rays which they otherwise could not utilize. How far this is connected with their living in deep water, which absorbs much of the red and yellow rays which are usually essential to photosynthesis in the green plants, has not been satisfactorily demonstrated.

The influence of light in affecting the form of the higher plants may be readily shown by experiment. The difference in habit between plants grown in dense shade and the bright sunshine is very marked, and while other factors than light are undoubtedly concerned, the light relation is one of the most potent factors in the change of form. The influence of light in determining the direction of growth of plants is familiar to every one, most plants growing towards the light, and in the lower plants, as well as the higher, this can be shown. In the flat gametophyte of the ferns and liverworts, the direction of the light striking it determines which is to be the upper and which is to be the lower side, and it has been recently shown by Peirce that in

some liverworts the dorsiventral character of the thallus can be inhibited by subjecting all parts of the developing plant to equal illumination.

**Relation of Photosynthetic Organs to Light.—**

In a general way the development of leaves, or the corresponding photosynthetic organs, is directly associated with the intensity of light, which up to a certain optimum is more and more efficient as the intensity increases. However, many plants are exposed to an intensity of light, and with it usually a degree of heat, which is in excess of the optimum, and, therefore, these plants have developed devices for protecting the delicate assimilating tissues from injury which might result from excessive illumination. The leaves may be covered with a very thick epidermis, which is sometimes supplemented by a sub-epidermal tissue of such character as to intercept much of the light and heat; or there may be special pigments developed, or the surface of the leaf may be covered with masses of hairs or scales which cover the exposed surfaces with a gray or white film.

In many tropical trees, like the mango, the young leaves are limp, and hang vertically, while they are colored pink or purple, both their position and the development of the special pigments being supposed to be methods of neutralizing the effect of the powerful sun's rays upon the delicate assimilative tissues of the young leaves. It is possible that the deep red or purple color of the young

leaves of tea-roses may have somewhat the same function. The vertical position of the leaves of Eucalyptus and of the Californian Manzanita, and the vertically placed phyllodes of the acacias already referred to, are also supposed to be protective devices against too powerful illumination. It is not easy to distinguish between modifications associated directly with excess of light, and those concerned merely with checking transpiration, which is increased by both light and high temperature.

**Climbing Plants.**—As light is the all-essential factor for the growth of green plants, it is not strange that the struggle for light in the teeming vegetation of the tropics has resulted in many adaptations. This explains the various types of climbing plants, which, although sparingly represented in the temperate regions, must be seen in the damp tropical jungles to appreciate their full possibilities. These climbing plants, either by twining their stems about others, or by lifting themselves up by tendrils of various kinds, may climb to the tops of the tallest trees, or stretch from one tree to another, often completely smothering the lower growths over which they spread themselves. Thus lifted above the lower vegetation, they expand their leaves and flowers in the full sunshine far aloft.

**Epiphytes.**—Another type of adjustment to light is seen in the Epiphytes, or air plants, which also are best developed in the tropical forests. In temperate climates most of the epiphytes are humble

plants like the lichens and mosses, but under more favorable conditions many flowering plants and ferns are found among these epiphytes. In the wet tropical forest, the trunks and branches of the trees, and even the surfaces of the leaves, may be covered with a tangle of liverworts, ferns, orchids, and even shrubs, like some of the rhododendrons and vacciniums. As these epiphytes are largely dependent upon the atmospheric moisture for their water supply, they are often more or less xerophytic in habit, having small thick leaves, or developing special water-storage organs, like the "pseudo-bulbs" of many orchids, and the water-storing scales of the Spanish moss and other bromeliads. A good many of the epiphytes, especially ferns, collect between their closely set leaf bases masses of humus, which serve both to hold moisture and to provide nourishment for the roots which ramify through the humus, and absorb nourishment from it.

**Light Not Always Necessary.**—While light is a necessary factor for the growth of all green plants, it is not essential for the existence of many forms without chlorophyll. Thus many bacteria normally live in complete darkness, and certain of the organs of green plants, especially the subterranean parts, develop in darkness.

Light exercises a powerful effect upon the development of many organs which are not connected with photosynthesis. The fruiting bodies of some fungi are not perfectly developed except in light,

and the degree of light often exercises a strong influence upon the production of the reproductive organs of many algæ. Many flowering plants, also, growing with insufficient light, develop few or no flowers.

**Nature of the Light Stimulus.**—The nature of the light stimulus is very obscure, and it is not likely that it is always the same. In some cases, e.g., where certain green spores refuse to germinate in darkness—it is quite probable that this is on account of the failure to develop certain products of photosynthesis before germination can begin, and this is made the more probable, as sometimes by supplying sugar, which might very well replace some of the products of photosynthesis, moss-spores may be made to germinate in darkness. The stimulus of light is not, however, indispensable in all cases, as many spores normally germinate in darkness, and apparently can develop the necessary stimulus for growth without the aid of light. The direct effect of light upon the rate of growth is usually a retardation. Plants growing in darkness become exceptionally elongated, and there is also a difference in the size of the leaves growing in shade and in full light. How far the larger size of the shade leaf is the direct effect of the action of the diminished light, and how far it is only a correlation, bound up with the necessity for a greater exposure of green tissue owing to the diminution of photosynthesis, it would be hard to say.

**Excessive Light.**—The effect of too strong light is injurious and may result in the destruction of the delicate tissues exposed to it. Hence arises the necessity in many plants for protection against excessive illumination, and as this is usually associated with high temperature, and consequently rapid transpiration, it is not always easy to determine how far certain structures are connected with excessive light, and how far with protection against heat and loss of water. Thus the thickened cuticle of the leaves, and the dense covering of hair often found in many plants exposed to hot dry air, are probably protective against both light and heat rays, and the same is true of the vertically placed leaves of *Eucalyptus* and *Manzanita*. This also holds good for the great reduction of surface seen in many plants of arid regions. In some species of broom and asparagus, and the cacti, the leaves are nearly or quite absent, and the small twigs develop chlorophyll in their outer tissues and replace the leaves. The amount of green tissue is thus greatly reduced, but the activity of these cells is much greater owing to the more intense light, and at the same time the transpiration surface is correspondingly reduced.

Certain effects apparently due directly to other factors may be found ultimately to be the result of light. Thus it has been found that plants having bright-colored flowers, when forced into bloom at high temperatures in a greenhouse, will develop pale-colored or even white flowers. Klebs, and others

who have investigated this phenomenon, have pointed out that the failure to develop the normal color in the flower may be attributed, not directly to the chemical effect of the light, but to the exhaustion of formative materials due to rapid growth incited by the high temperature. The photosynthetic activity, owing to the weakness of the illumination, is not sufficient to provide the extra material needed for the development of the normal pigment in the flowers, but this is used up in the growth of the plant. If the same plants are grown where it is cooler, and growth therefore less active, while the illumination is equally strong, pigment will reappear in the flowers. The light, therefore, does not directly cause the production of the pigment, but, by promoting photosynthesis, allows for the accumulation of the substances necessary for the development of the pigment.

## FUNGI

**Fungi Either Parasites or Saprophytes.**—Whatever may have been the origin of the Fungi, they differ radically, both in their structure and habits, from the green plants, and show many unmistakable instances of special adaptations. They subsist largely upon solid organic matter, such as the living bodies of plants and animals, or dead substances like decayed wood and vegetable mold. The plant body consists of fine filaments, or hyphæ, which by

the development of active ferments, or enzymes, are able to penetrate the most resistant organic substances, like wood, or the chitinous armor of insects. This ability to destroy organic bodies makes the fungi of some importance in the decomposition of organic matter, although their rôle in this respect is much less important than that of the bacteria.

Many of the parasitic fungi, like the black knot of plums, or the onion mildew, cause abnormal growths, sometimes resembling the galls formed by insects. Whether these hypertrophied growths are due to mechanical irritation, or to the effect of enzymes secreted by the fungus, or to some other chemical stimulus, is not certain. But the abnormal growth is presumably advantageous to the parasite, as the food supply must in this way be notably increased.

**Symbiosis.**—While most parasitic fungi are very destructive to their hosts, sometimes killing them outright, there is a modified form of parasitism which is of common occurrence. This is known as Symbiosis, and is a phenomenon of much wider occurrence than was formerly supposed. The nitrogen-fixing bacteria have been referred to in a former chapter, and it now seems certain that a considerable number of fungi can also utilize free nitrogen, and are of material assistance in supplying nitrogen to certain plants with which they live symbiotically. They are often associated with the roots of many flowering plants, especially certain trees like the

beech, and many species growing in humus, such as some of the Heath family, e.g., species of rhododendron and huckleberries. In such saprophytes as the Indian-pipe (*Monotropa*), and the coral-root orchids, which are without chlorophyll, the fungi furnish not only nitrogen, but also carbon in some form. It seems likely that the carbonaceous matter from the humus is first elaborated by the fungus, which is then itself destroyed within the tissues of the host. There seems to be a sort of mutual parasitism. The fungus at first feeds upon the host, which afterwards retaliates, and destroys the fungus within its tissues.

The most familiar case of symbiosis is that of the lichens, where a fungus and an alga are intimately associated. While in this association the fungus undoubtedly behaves as a true parasite toward the alga, which under favorable conditions can grow quite independently, there seems no reason to doubt that the alga itself derives some benefit from its association with the fungus. Within the sheltering tangle of fungus filaments it is supplied with water, and it is quite probable that a certain amount of nourishment, presumably of a nitrogenous nature, is also supplied to it.

***Synchytrium papillatum*.**—That many parasitic fungi are of comparatively recent origin is certain, as some species may be associated with a specific host, which is often a highly organized and presumably a recent type of flowering plant, and the

specific characters of the parasite must have been developed as late, at least, as those of the host. A curious case is that of the parasitic fungus, *Synchytrium papillatum*, which at present is known only from California, where it sometimes grows abundantly upon a weed, *Erodium*, which is supposed to have been introduced from Europe, not more than two hundred or three hundred years ago. The fungus is not known to occur in Europe, nor has it been found upon any native Californian plant. It would be interesting to know, whether we have a new species arising from some native fungus which has adapted itself to a new host, and thus developed new specific characters, or whether it is merely a case of an imported fungus which has developed more luxuriantly in its adopted home.

How far the more or less complete suppression of the sexual reproduction, which has been observed in so many of the fungi, is due to degeneration, consequent upon their habits, is not possible to determine.

### STORAGE ORGANS

In the economy of the plant it often becomes necessary to provide storage organs upon which the plant can draw at certain times. This is seen in its simplest form in the spores of the lower plants, which are packed with various nutritive substances like starch and oil, which fur-

nish the materials for the first stages of germination. In the higher plants the seeds contain similar stores of food, either in the endosperm or less commonly in the outer seed-tissues, or in the tissues of the embryo itself. Other types of storage organs are bulbs, tubers, root-stocks, etc.

### PARASITES AND SAPROPHYTES

The great group of fungi are all either parasites or saprophytes, and among the flowering plants there are also found many species which have become more or less completely parasitic or saprophytic, but the latter are probably all derived from forms originally possessing chlorophyll. Parasites and saprophytes are not common among the archegoniates, but there are a number of examples known. Where plants are completely parasitic or saprophytic there is a complete loss of chlorophyll, and with it a more or less extensive degeneration of the leaves. The humus saprophytes may also have their roots replaced by root-like stems. These differences are evidently correlated with the marked changes in the method of nutrition.

**Parasitic Flowering Plants.**—The normal green plant derives most of its food from the inorganic substances  $\text{CO}_2$  and water, together with certain nitrogenous and other elements absorbed from the soil. There are, however, many plants which are

dependent to a greater or less degree upon other organisms for their substance. It is among the higher flowering plants that the most remarkable parasites and saprophytes occur. The most extreme parasites are found in certain tropical and subtropical species, of which the extraordinary *Rafflesia* of Sumatra may be taken as a type. This parasite passes the whole of its vegetative existence within the tissues of its host, a species of wild vine, and the vegetative structures of the parasite are so reduced, that they more nearly resemble the mycelium of a fungus than the body of a normal flowering plant, and the parasite feeds upon its host somewhat in the same way that the fungus does, the tissues being in direct communication with the conducting tissues of the host. At maturity enormous flower buds are formed, which burst through the outer tissues of the host, and the gigantic flower expands and develops its seeds exposed to the air. The extraordinary degradation of these endoparasitic flowering plants makes it very difficult to ascertain their relationships. Complete parasitism, but less extreme, is met with in a good many more or less familiar plants. The dodder is one of the best-known forms, and is a genuine parasite upon a variety of other plants, twining its leafless stems about them, and sending suckers into the host from which it derives all its nourishment. The leaves are reduced to scales and only a slight trace of chlorophyll can be detected. Many of these para-

sites grow upon the roots of other plants, e.g., beech-drops (*Epiphegus*), canker-root (*Aphyllon*), and others. Certain parasites may not be entirely dependent upon their host for carbon, being able to assimilate  $\text{CO}_2$ . Of these parasites the various species of mistletoe are the best-known examples, and a number of the Figwort family are also known to be root parasites, although these have well-developed roots. Of these green root-parasites *Gerardia* and *Castilleia* may be mentioned.

**Saprophytes.**—There are many saprophytic flowering plants, these being especially numerous in the Heath family, and among the orchids. Saprophytism may be present in plants having green leaves, like species of rhododendron and many others; while in others all chlorophyll has been lost, and the leaves and sometimes the roots are rudimentary. The coral-root orchids, the Indian-pipe, and the curious snow-plant (*Sarcodes*), of the Sierra Nevada, represent this extreme case of saprophytism. In all of these, so far as they have been investigated, there is always associated a fungus, by means of which they seem to be able to utilize the necessary carbon compounds from the humus. This peculiar form of parasitism, symbiosis, has already been referred to. The exact nature of this association is not always clear, but its constant occurrence implies that the association is mutually beneficial. In the lichens the association is so intimate that the resulting structure has assumed

the form and character of a distinct organism. There is no doubt that the fungus element is parasitic upon the alga, upon which it is dependent for its existence, but the alga seems to suffer little from its imprisonment in the tissues of the fungus, and as the latter takes up water very quickly and retains it tenaciously, the alga is undoubtedly enabled to grow, thanks to the shelter of the fungus, where otherwise it could not exist. Moreover, the recent evidence that some of the higher fungi, as well as bacteria, can assimilate nitrogen, makes it quite probable that the fungus gives to the alga certain nitrogenous compounds in return for the carbonaceous food taken from it. It is likely that in the case of the association of the fungus with a saprophytic flowering plant, nitrogen is also furnished to the host as well as carbon.

The symbiotic association of two green plants is much less common, but a good many cases are known. Usually one of the symbionts is a blue-green alga, and it is possible that here also there may be a case of nitrogen assimilation which may be useful to the other party of the association. A number of liverworts, e.g., *Blasia*, *Anthoceros*, have always associated with them a species of *Nostoc*, and the little water-fern, *Azolla*, always harbors in its leaves colonies of a blue-green alga (*Anabæna*). No actual parasitism has been shown in any of these cases, and just what the relation of the two symbionts is we really do not know.

**Carnivorous Plants.**—A most extraordinary form of adaptation is that of the so-called carnivorous plants, of which a number of remarkable types are common in the United States. These are either aquatics or bog plants, and it is supposed that their peculiar habits are due to a deficiency of nitrogen in their environment. In the sundew (*Drosera*), butterwort (*Pinguicula*), and Venus's flytrap (*Dionæa*) the leaves are modified into traps, which capture small insects alighting upon them, and after the insect is secured, there is an actual digestion by the aid of digestive ferments not unlike those found in the digestive organs of animals. A similar ferment has been demonstrated in the pitchers of the Asiatic pitcher-plant (*Nepenthes*). In the American pitcher-plants (*Sarracenia* and *Darlingtonia*), and in the bladder-weed (*Utricularia*), the leaves form traps into which the insects are lured, but there is very little or no digestive effect upon the bodies of the victims, which are drowned and the products of their decomposition are absorbed by the leaf. These carnivorous, or insectivorous, plants are among the most extraordinary examples of special adaptation that are met with in the whole vegetable kingdom.

#### PLANTS AND ANIMALS

As plants are essential to the existence of all animal life, it is not remarkable that the structures of

animals should often show evident adaptations to plant structures. The mouth parts and the digestive organs of herbivorous animals, the beak and tongue of humming-birds, the mouth part of many insects, are a few of the most common examples. But it is equally clear that certain modifications of plants have also been induced by their relation to animals. The most remarkable of these adaptations are associated with the employment of animals as agents in pollination and seed distribution.

Of course it is impossible to say just how far the relation of animals to plants has acted directly upon the structures of the latter, but it is very evident that whatever may have been the inducement of certain structures, the preservation and perfecting of these characters have been very potent factors in aiding the plants in the struggle for existence. Thus the grasses have been extraordinarily successful in holding their own in competition with other plants in nearly all parts of the world, and at the same time they form perhaps the most important of all food plants for the higher animals. In common with many other monocotyledons, the leaves frequently possess an unlimited power of basal growth, and may be cropped repeatedly without injury; moreover, many grasses are characterized by an extraordinary power of rapidly spreading by means of underground stems or runners. It would perhaps be rash to assert that these habits have arisen in response to a need for protection against the rav-

ages of grazing animals, but there is no question that these peculiarities have enabled the plants to survive and flourish, in spite of constant cropping.

**Protection Against Animals.**—Somewhat different are the special protective devices found in many plants which enable them to repel the attacks of animals. These are especially marked in plants of arid regions where the life conditions are precarious. The development of defensive armor, like the terrible spines of the cacti, and the dagger leaves of the century plant and yuccas, as well as the rank secretions of the sage-brush and creosote-bush, are very efficient weapons against the attacks of hungry animals; and although they may be only physiological responses to the arid environment, they are nevertheless exceedingly useful to the plant as protective measures, and must have been of immense importance in preserving plants in the very unfavorable conditions surrounding them.

**Myrmecophily.**—The insectivorous habit of certain plants has already been referred to, but another extraordinary association with insects may be briefly cited, as it is one of the most remarkably reciprocal adaptations known to the naturalist. This is the habit discovered in certain ants of associating themselves with plants in a sort of symbiotic relation, which has been termed “myrmecophily.” In a number of trees, notably the genus *Cecropia* in tropical America, and certain species of *Acacia*, the trees harbor colonies of ants which inhabit

their hollow stems, or in the case of the *Acacia*, much enlarged hollow thorns. These trees are subjected to the attacks of leaf-cutting ants, which are repelled by the ants living in the trees, whose foliage is thus saved from destruction. Sometimes the trees furnish not only lodging but also board, as there are developed certain peculiar secretions which serve as food for their insect tenants.

A remarkable form of myrmecophily has been recently studied by Wheeler in a number of ants from Texas and other warmer parts of America. These ants carry into their nests masses of leaf-fragments which they pack together so as to form a sort of miniature hotbed. Upon this mass of fermenting vegetation there soon appears a peculiar fungus, which grows luxuriantly and produces food bodies upon which the ants feed.\*

## REPRODUCTION

**The Necessity for Reproduction.**—The necessity of some form of propagation for the perpetuation of the species is evident, and many types of reproduction have developed in response to this need. The simplest of all is the ordinary cell fission, the only

\* Professor Wheeler, in his recent book on the structure and habits of ants, has expressed some doubt as to the entire accuracy of some of the observations made upon the habits of the tree-dwelling ants. He believes that the adaptations between the ants and the host tree are not so complete as have been assumed.

type of reproduction in many of the lowest organisms. Usually, however, there are developed more or less specialized cells, whose sole function is reproduction. In many algæ these reproductive cells escape from the parent cell and become free-swimming zoöspores, which settle down and grow into new plants directly. The advantage of the motile condition for the distribution of the species is evident enough.

Sudden changes in the environment may act as powerful stimuli in inducing the formation of reproductive organs. It has been shown that algæ in running water grow vigorously, but seldom or never develop their reproductive cells; but when transferred to still water they will often develop zoöspores in very great numbers. Some algæ which live in the air will quickly form zoöspores on transferring them to water. Light, temperature, changes in the food—all of these act as stimuli in controlling the reproductive processes. Thus in the water-net (*Hydrodictyon*), plants grown in a solution of cane sugar will produce an enormous number of gametes.

While in many of the lower plants reproduction is purely non-sexual, most algæ produce some form of gametes, or sexual cells. These are evidently modifications of originally non-sexual cells, or zoöspores, and it is sometimes impossible to certainly distinguish between the two. While usually there is a fusion of the gametes, they may develop without union under certain conditions,

and this parthenogenesis may be the result of changed conditions; for example, increase of temperature, or cultivation in a special nutritive medium.

**Resting Spores.**—Very commonly the zygote resulting from the union of the gametes is a resting cell, or spore, which is adapted to resist the desiccation to which fresh-water algæ are so frequently exposed. It may be assumed that the various forms of thick-walled resting cells, developed by fresh-water algæ, are adaptations to drying up, as these are very seldom met with in the marine algæ, where drying up, of course, never occurs. The connection of these resting spores with the origin of the lower land plants has already been pointed out.

**Spore Distribution by Insects.**—It is in connection with reproduction that plants have been most profoundly influenced in their structures through association with animals. Among the lower plants this is far less marked than is the case among the flowering plants, but there are a number of cases of apparent adaptation to animal agencies in spore distribution. Of course the accidental distribution of spores and other minute germs, which adhere to the bodies of animals, must constantly occur, but there are several cases where this seems to be especially provided for. Thus in the fungus which causes the disease known as Ergot upon rye, at a certain stage in the development of the fungus there is produced a sweet substance which attracts insects, to which the spores adhere and are presuma-

bly thus disseminated. The slimy spore masses of the Phalloideæ, a family of large fungi, have an excessively offensive odor which is said to attract carrion-loving insects, which are the disseminators of the spores which adhere to their bodies. It is among the angiosperms, however, that the most perfect instances of these adaptations are found.

**Cross-pollination by Insects.**—While there has lately been a tendency to minimize the importance of insect aid in the pollination of flowers, and to explain otherwise their remarkable color devices and structures, there can be no question that the extraordinary development and diversity of the angiosperms is, in a very large measure, the result of their adaptations to cross-pollination through insect agency. Cross-pollination is known to be distinctly advantageous in many cases. The seeds of cross-pollinated flowers have been shown by Darwin and other investigators to be more numerous and better developed, and the resulting seedlings distinctly larger and more vigorous, than those derived from seeds from self-pollinated flowers. Moreover, a good many flowers, e.g., many orchids, have been found to be quite sterile with their own pollen, which may even act injuriously upon the pistil. It is also a legitimate assumption that the increased variability due to cross-pollination is an advantage, as tending to cause new characters to appear which may be taken advantage of by natural selection.

The lower types of flowers, such as those of

nearly all gymnosperms and the apetalous angiosperms like the oaks and most grasses, are generally dependent upon the wind for distributing their pollen, which is light and produced in very great quantities, and is readily borne long distances through the air. Cross-pollination is often the rule, however, even here, as the flowers are frequently "diclinous," that is, have their stamens and carpels in different flowers. Wind pollination involves a great waste of pollen, as probably not one pollen-spore in a million is efficacious. It is clear that a material saving in the amount of pollen and its increased efficiency ought to be of advantage to the plant.

Pollen cells are rich in nutritive matter, and hence are sought for as food by many insects. It may be supposed that the first cases of insect pollination were purely accidental and brought about by the search for pollen as food. If for any reason any flowers should be more conspicuous than others, it is quite conceivable that they would more readily attract the attention of visiting insects, and it is quite conceivable also that through some increased size of the enveloping leaves, or brighter color of the stamens, the line of evolution started which culminated in the gorgeously colored and highly specialized flowers of many of the orchids and Compositæ.

In the lower types of flowers the enveloping leaves are inconspicuous scales, serving merely

for protective purposes; but we soon meet with flowers in which these are replaced by more or less conspicuous floral leaves. It is safe to say that no showy flower is entirely destitute of insect visitors, although it may not be absolutely dependent upon them for its pollination, and cross-pollination must occur in a great many cases. If cross-pollination is prevented, however, many flowers are capable of pollinating themselves. Such flowers as the buttercup or anemone and the inflorescences of many *Compositæ*, like the dandelion, are of this character. In the latter case, however, cross-pollination of a sort really does occur, as we have to do, not with a single flower, but with a group of flowers in which each individual flower is likely to be pollinated from another one.

**Specialization of the Flower.**—In the simpler hermaphrodite floral types, such as the water-lily or magnolia, there is a multiplication of parts and an indefiniteness in their number that is in strong contrast to the very definite structures of such a flower as a foxglove or orchid. This definiteness of structure involves a reduction in the number of certain parts (see chapter on Angiosperms for details), and later a cohesion of the floral organs. This begins with the carpels, which in a majority of the higher plants are fewer in number than the other organs, and are more or less completely united into a compound pistil. Next follows the reduction in the number of stamens, which reaches its maxi-

mum in certain highly specialized monocotyledons like the orchids and canna, where usually only a single functional stamen is present. Where the number of stamens is reduced, this is almost always associated with change from the original radial symmetry of the flower to a marked bilateral symmetry. This is seen in the cases cited and also in such dicotyledons as the mints and bignonias, in which the floral leaves are united into a tubular or trumpet-shaped corolla.

**Color and Scent in Flowers.**—With these modifications in structure there are associated a great variety of vivid colors, so that these specialized flowers include most of the more showy species under cultivation. Another common phenomenon is the development of the characteristic scents in flowers, these being, in the opinion of many modern students of cross-pollination, the most potent means of attracting insect visitors. Color and scent may both be associated with the secretion of nectar, the principal object of the visits of butterflies and many other insects.

How far insects are able to discriminate the colors of flowers, and especially the elaborate color-patterns of the so-called "honey guides," etc., is much in need of thorough investigation. While the earlier investigators attributed to insects a capacity for color discrimination not entirely warranted by the facts, there is no question that the conclusions of some of the recent oppo-

nents of these views go too far in the other direction, and are quite as much in need of further confirmation. It may be safely asserted that any showy flower is normally pollinated by insects, and there is, moreover, no question that color is in some cases directly an adaptation. The pale color of most night-blooming flowers is an obvious adaptation, making the flowers more conspicuous in the dark or twilight, and it is equally evident that the strong scent of many of these nocturnal flowers is also a powerful lure to the insects visiting them. Some of the nocturnal flowers, which are quite scentless in the daytime, exhale a very strong perfume in the evening. This is especially true in some of the Nightshade family. The long-tubed flower of the white petunia and the white-flowered tobacco, often grown as an ornamental plant, flood the garden with their strong perfume soon after sunset, and the odor wafted from the big trumpets of the tree *Datura* is almost overpowering. These tubular nocturnal flowers are especialy frequented by the great humming-bird moths, whose enormously long tongues are especially fitted for probing their nectaries.

While such showy flowers as the magnolias and buttercups, which are normally insect pollinated, can, if necessary, pollinate themselves, this is not the case in a great many flowers, which are so constructed that cross-pollination is absolutely necessary. Only a brief reference can be made to

a few of the more striking cases. For a fuller account of these special contrivances to insure cross-pollination the reader must be referred to the works of Darwin, Kerner, Müller, and other students of these interesting problems.

**Prevention of Self-fertilization.**—One of the common methods by which cross-pollination is secured, is the maturing at different times of the stamens and carpels. A common example of this is seen in the scarlet geranium, where all the pollen is shed before the pistil is ready to receive it, so that the flower must be pollinated from a younger one, and this must be done through the aid of insects. In the nasturtium much the same conditions exist, but the pistil, when it is ready to receive the pollen, takes a position exactly the same as that occupied by the stamens at the time that the pollen is shed, so that the bee or humming-bird, coming from the younger flower, and bearing with it the pollen, touches the same part of the body to the pistil in the older flower, and thus deposits upon it the pollen which it has brought from the younger one (Fig. 21, C, D).

**Heterostylism.**—In a number of plants, including species of primrose and some of our native plants, e.g., the trailing arbutus and partridge-berry, what is known as heterostylism occurs, i.e., there are pistils of two lengths in different flowers, and the stamens are of reciprocal lengths. Thus long-styled flowers have short stamens, and *vice versa*.

This usually ensures the pollination of the pistil of a flower with pollen from stamens of corresponding length, taken from another flower.

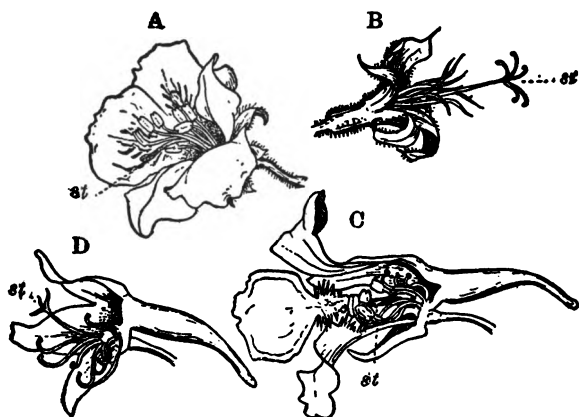


FIG. 21

A—Recently opened flower of *Pelargonium*; the stamens are ready to discharge the pollen, but the stigma, *st*, is still immature.

B—An older flower of *Pelargonium*, with the petals removed; the anthers have fallen, and the stigma is open and ready for pollination.

C—Section of a young flower of *Nasturtium*; three of the seven stamens have discharged their pollen; the others are nearly ready to do so, but the pistil, *st*, is still immature.

D—Older flower; all the stamens have discharged the pollen and bent down; the ripe pistil now occupies a position in front of the open spur, where it will receive pollen brought from a younger flower.

**Cross-pollination in Orchids.**—The orchids probably show the most extraordinary adaptations for

cross-pollination, their flowers being often absolutely sterile unless the proper insect visitors are available. One of the simplest cases is seen in the genus *Orchis* (Fig. 22). In *Orchis*, and the same is true of very many other orchids, the

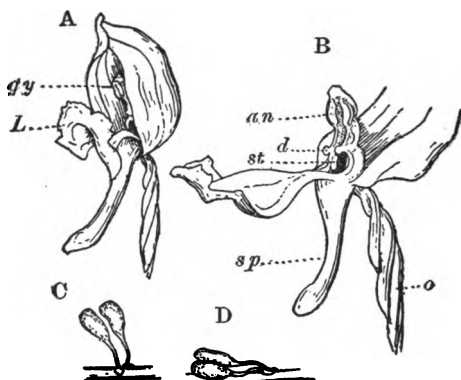


FIG. 22

A—Flower of *Orchis spectabilis*; *L*, the lip; *gy*, the column or gynostemium.

B—A flower with the upper segments bent back so as to expose the column; *an*, the anther; *d*, adhesive disc of the pollinium; *st*, one of the stigmatic surfaces; *sp*, the spur; *o*, ovary.

C—The two pollinia, adhering to a slender straw thrust into the flower.

D—The same pair of pollinia, a few minutes later, showing the change of position; if the straw is now thrust into the flower, the pollinia will come in contact with the stigmatic surfaces.

pollen is aggregated in small masses, or pollinia. These pollinia are held in little pockets, or recepta-

cles, from which they must be forcibly removed by the agency of the insect which visits the flower for the nectar. As the insect enters the flower, the cover of this receptacle is ruptured and the packet of pollen is withdrawn and adheres firmly to the head or tongue of the insect. After the pollen mass is withdrawn, it often shifts its position so that it will come into contact with the stigmatic surface of the next flower visited. In this case, as in most flowers with deep nectaries in the form of a long spur, the honey can only be extracted by insects with long tongues, like butterflies and bees, and the extraordinary mouth parts of these insects are beyond any question adaptations for feeding upon the nectar of flowers having these deep nectaries.

**Pollination of Yucca.**—One more example must suffice, as perhaps the most peculiar adaptation to cross-pollination that has yet been studied. In the warmer parts of the United States there are several species of the genus *Yucca*, comprising a number of showy lily-like plants, of which some are not uncommon in gardens. In nearly all of the species that have been studied there has been found a most extraordinary case of special adaptation, these plants usually being dependent for pollination upon a single species of moth, of the genus *Pronuba*. The first species which was described, *P. Yuccasella*, pollinates the common species of *Yucca*, *Y. filamentosa*, in the Southeastern United States. The larvæ of these little moths feed upon the young seeds of the

*Yucca*, and the parent moth lays her eggs in the ovary of the open flower, and then collects a mass of pollen and forces it down the central part of the stigma, thus ensuring fertilization of the ovules, and the provision of a future food supply for the larvæ. The latter do not devour all of the seeds, some of which are left, which pay for the seeds devoured by the larvæ.

**Birds as Agents in Cross-Pollination.**—While insects are the main agents in cross-pollination, other animals may be more or less important. Occasionally snails have been found to act as agents in pollination, but next to insects, certain families of birds are of the first importance. In the warmer parts of the Old World, the honey-suckers or sun-birds of the large family *Cinnyridæ*, are flower visitors and are especially adapted to extracting the honey from flowers, and undoubtedly like insects they carry pollen from one flower to another. More important still are the humming-birds of the New World. They are distributed practically over the whole American Continent, from Alaska to Patagonia. They are preëminently flower visitors, and very many of our native flowers are clearly adapted to their visits. These “ornithophilous” flowers are usually very vividly colored, bright red seeming to be the commonest color. A host of tubular scarlet flowers like the canna, scarlet sage, nasturtium, fuchsia, scarlet columbine, trumpet creeper, etc., are prime favorites of these little feathered gems.

In his studies of the ornithophilous flowers of South Africa, Scott-Elliot calls attention to the preponderance of bright red or orange color in the flowers which are frequented by the sun-birds. These belong to often widely separate families, both monocotyledons and dicotyledons. He states, also, that there seems to be a relation between the color of the birds and that of the flowers, the red color in the species of *Cinnyris*, a genus of honey-sucker, being almost exactly identical with the shade of red found in a majority of the ornithophilous flowers. I have seen myself, in South Africa, the sun-birds visiting the scarlet *Erythrina*s and *Aloes*, and Scott-Elliot gives a long list of other similarly colored flowers which are frequented by these birds. In their small size and colors, many of these sun-birds recall strongly the iridescent American humming-birds, although they are not at all related.

While we may hesitate to accept all the conclusions of the enthusiastic students who first realized the immense importance of insects in the pollination of flowers, there seems to be no reason to doubt that the course of evolution of the two largest groups of animals and plants, insects and angiosperms, has been powerfully influenced by the mutual adaptations that have arisen in these two groups of organisms.

## CHAPTER VIII

### THE PROBLEMS OF PLANT DISTRIBUTION

**T**HE origin of the existing flora of the earth is lost in the obscurity of an enormously remote past. We have practically no knowledge of the lower plant types from the earlier geological formations, which is not surprising when we remember the extreme delicacy of these very perishable organisms; and the first plant remains that can be identified belong to species relatively high up in the scale of development, and must have been preceded by countless forms of lower rank.

**Antiquity of the Principal Types of Plants.**—It is evident from a study of the fossils of the Paleozoic, that nearly all of the living plant types, except the highest forms of seed-plants, were already in existence during that period. Ferns and primitive seed-plants occur in the Devonian, and these reach a high degree of development during the Carboniferous. While few traces of the less resistant plant types, such as the seaweeds and mosses, are met with, enough of these have been found to show, as might have been expected, that these plants also

existed during the early geological ages, and probably were not very different from their living descendants.

**Uniformity of the Early Floras.**—A notable feature of the primitive floras of the earth was their uniformity. While at the present day different regions possess very different floras, during the Paleozoic era there seems to have been a practically uniform flora throughout the greater part of the earth. There is very little difference between the Paleozoic fossils found in the arctic regions, and those which occur in tropical beds, this being especially true of the Carboniferous fossils.

**Paleozoic Climate.**—Various explanations of the apparently uniform climate that seems to have prevailed have been made, one of the latest, and one which has a good deal of plausibility, being that of Manson, who believes that during the earlier geological epochs the earth was enveloped in a dense layer of clouds which neutralized the effects of the solar rays, the heat being mainly the result of direct radiation from the earth itself, which would thus have practically a uniform climate throughout its whole extent. If this view is correct, it would have to be assumed that the cloud envelope was sufficiently transparent to admit enough of the light rays for the existence of green plants. But it must be remembered that the plants of this period, to judge from the fossils, were mostly forms which are able to grow with a limited amount of light, and

which do not require light for the development of their chlorophyll. In the later geological time, according to this theory, the layer of clouds was gradually dissipated, and the zonal climates, as they now exist, were by degrees established. From a study of the plants of the Paleozoic, especially of the Carboniferous, which have left recognizable descendants at the present time, we may conclude that the climate was a moist one but not necessarily extremely hot. The pteridophytes, which were the predominant type, at the present day reach their most perfect development in the wet mountain forests of the tropics, where the temperature is even, but not excessively high.

**The Lower Plants Have Left Few Fossil Remains.**—The early history of the lower plants can only be conjectured. It is pretty generally conceded that the simple green algæ represent more nearly than any other living plants the ancestors of the present land flora. Whatever may have been the origin of the red and brown algæ, it is clear that they are relatively modern forms, which are especially fitted for marine life. Little is known of the early geological history of the fungi, but traces of these are sometimes met with and there is reason to suppose that they were abundant during these early times.

Both the simple green algæ and lower liverworts show evidences of their primitive nature, and probably are little changed descendants of their ancient

prototypes. These forms, although comparatively few in number at the present time, are of remarkably wide distribution, many of the genera being cosmopolitan. The distribution of the liverworts is especially interesting in this connection, and in most cases can be explained only on the hypothesis that they are survivors of widely distributed types, which have come down probably from the Paleozoic with little change. This is especially the case in such tropical genera as *Dumortiera* and *Monoclea*.

**Fossil Pteridophytes.**—The history of the Pteridophytes is much easier to trace, as there are abundant fossil remains, evidently closely related to many living types, and indeed some living genera can probably be traced back to the Paleozoic. The Paleozoic ferns are for the most part of the so-called "eusporangiate" type, and are allied to the living ferns of the family *Marattiaceæ*, which at present are found mainly in the tropics. While many of the "ferns" of the Paleozoic are now known to be seed-bearing plants, there is no reasonable doubt that true ferns, allied to the *Marattiaceæ*, were abundant in the Paleozoic flora.

**Climatic Changes in the Permian.**—The last period of the Paleozoic, the Permian, was an era of transition. There are evidences of severe glaciation in the Southern Hemisphere, and less marked glaciation in many regions in the Northern Hemisphere, where in a good many places it is also evident that marked aridity prevailed, in strong contrast to the

very humid climate, which seems to have characterized most of the Carboniferous. There seem to have been two great land masses in existence, a northern and a southern one, and the floras of the two were different in many ways. Thus the Southern Hemisphere was characterized by a type of fern, *Glossopteris*, which was accompanied by a number of other peculiar southern types (see Scott: "Studies in Fossil Botany"). It was probably during this transition period, between the Carboniferous and the early Mesozoic, that the modern cycads and conifers first became prominent. These plants are most of them more or less xerophytic, and the increased aridity of the climate of this period may very well have been the cause of the ascendancy of these plants over the moisture-loving pteridophytes of the preceding geological epoch.

**The Highest Types of Plants Arose in the Mesozoic.**—The second great geological epoch, the Mesozoic, is supposed to have been of much briefer duration than the Paleozoic, but it is noteworthy as the time in which the highest groups of plants and animals came into existence. Birds and mammals, on the one hand, and the angiospermous flowering plants on the other, made their appearance during the Mesozoic. The warm but dry climate of the early Mesozoic seems to have been especially favorable to the cycads, which at that period reached their culmination, giving place later to the more modern conifers and angiosperms. During the latter part

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of the Mesozoic, especially the Cretaceous, the climatic conditions were apparently less uniform than at the beginning, and zonal climates were already indicated, although much less pronounced than at present.

Quite suddenly toward the end of the Mesozoic, in the Sub-Cretaceous, the angiosperms, the highest of all plants, first appear. Their origin is very obscure, but once developed, they show an extraordinary power of adaptation, and soon outnumber all the other plants, increasing their supremacy until now they are by far the most important of living plants. The earliest seed-bearing plants, the Cordaitales and Pteridosperms, became extinct towards the end of the Paleozoic, and were replaced by other types which have persisted down to the present time. The Cycads, Ginkgoales, and the lowest Conifers were probably all in existence before the end of the Paleozoic.

During the whole of the Mesozoic, North America was connected with the Eurasian Continent, and although this connection was probably broken down during the Tertiary, it was reestablished from time to time, so that there was free intermingling of the floras throughout the whole extent of the Northern Hemisphere, and this flora maintained its similarity up to the end of the Tertiary.

**Cretaceous Plants.**—A good many existing genera occur in the Cretaceous, and it would seem from their distribution that the climate of the Northern

Hemisphere was still warm, and more uniform than at the present time. Many familiar modern genera flourished, and while these Cretaceous fossils are almost entirely trees or shrubs, it is only reasonable to suppose that many widespread herbaceous genera, like *Ranunculus* and *Geranium*, also existed at the same time. Among the early Cretaceous types may be mentioned poplars, willows, and planes. Certain genera, which now are represented by isolated species in remote regions, were at that time widespread; such for example are the tulip-tree (*Liriodendron*), *Magnolia*, and *Sequoia*, which once occurred throughout much of the Northern Hemisphere. These survivors of the late Mesozoic and early Tertiary floras are at present mostly confined to warm-temperate regions, such as Japan, the warmer Atlantic States, and the mountains of California, and suggest that the climates of these regions represent approximately the climate of that period.

The number of angiosperms rapidly increases during the Tertiary, and very many of our common genera of trees and shrubs are clearly recognizable. Oaks, maples, walnuts, sassafras, and other familiar forms, all very much like existing species, are met with, and we may suppose that many of the common herbaceous types, which now accompany these, were also in existence, although owing to their perishable nature they have left no recognizable fossil remains.

#### FACTORS CONCERNED IN PLANT DISTRIBUTION

The factors that have been active in determining the distribution of the existing floras of the earth are many and complicated. Some of them are sufficiently clear, but of many we are quite ignorant at present. Of the most obvious conditions, probably climate, i.e., temperature and moisture, is of most importance; but several other very evident factors may be mentioned which play parts quite as important in the distribution of plants. These are the continuity of land areas, composition of the soil, and the exposure of the soil. But perhaps most important of all are the individual characters of the plants concerned, some being especially adaptable and provided with ready means of transportation, others very particular as to their requirements of growth, and therefore confined to extremely limited areas. It is the underlying causes of these great differences in the very constitution of different plants, that are the most obscure and little understood factors governing plant distribution.

**Uniform Flora of Northeastern United States.**—Where there are extensive areas with uniform climatic conditions, and no barriers to prevent ready communication, the flora will be found to be very similar, varying only with the local peculiarities of soil or elevation. The Northeastern United States is an excellent example of such an area. A very large number of species occur throughout the entire

region, and the greater richness or poverty of species in different localities is due only to local conditions. The prevailing trees, pines, hemlocks, oaks, maples, elms, hickories, beeches, etc., are the same everywhere, the flora naturally being richer in the warmer and moister southern portions than in the colder and drier northwest. The shrubs and herbaceous plants are much the same throughout, of course taking into account the local differences of soil and exposure.

**Effect of Varying Rainfall in Jamaica.**—The general uniformity of such a flora as that just sketched has only to be contrasted with the flora of a very much smaller area, where for special reasons adjacent districts differ much in climate, especially in the amount of rainfall. In Jamaica, for instance, within a distance of about forty miles, mountains rise to a height of over 7,000 feet, and cause the precipitation of most of the moisture upon one side of the range, the northern side receiving from three to four times as much rain as the southern side does, only forty miles away. The result is that the vegetation of these two areas is more different than that of Chicago and New York, nearly a thousand miles apart.

At Kingston, on the southern shore of the island, the dry plains and hillsides recall our southwestern arid region, the prevailing plants being decidedly xerophytic in character. Thus cacti, century-plants, mesquit, and many other plants, belong-

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ing to a distinctly arid region, are the conspicuous features of the flora. At Port Antonio, on the northern shore, there is a veritable tropical jungle; the trees are laden down with heavy creepers, and dense masses of epiphytes, and aroids, wild ginger, palms, peppers, bananas, and many other representatives of the wet tropics, crowd the spaces between the creeper-laden trees. Of course in a tropical region the differences would be much more marked than in a temperate one, where the conditions for plant growth are so much less intense.

The amount of moisture and the character of the soil have very much to do with determining the vegetation of any area. The differences between the flora of a swamp, and that of a dry hillside in the immediate neighborhood, are complete, and probably no single plant will be common to both. The floras of peat bogs are almost always exceptionally peculiar. While many plants are quite unable to live in these, there are others which have adapted themselves to the very peculiar conditions of the bog and refuse to grow elsewhere. Some of the most beautiful orchids, the pitcher-plants, and sundews belong to this category.

**Character of Soil a Factor in Distribution.**—The question of soil is a very complicated one and involves numerous factors. Many plants are exceedingly sensitive to the character of the soil in which they grow. Thus many of the Heath family,

Azaleas and Rhododendrons, avoid soils containing lime, while for many other plants lime is an essential. The mechanical characters of the soil, that is, whether it is compact or loose, retentive of water or the reverse, are also important factors in determining the distribution of many plants. Finally the special devices, like winged seeds and fruits, play an important part in determining the distribution of some plants. Most weeds are such because of the facility with which they can be distributed. With this facility for distribution there also goes the hardiness and adaptability which these plants exhibit. One has but to contrast the dandelion with such an orchid as *Arethusa*, for example, to realize the difference between a really adaptable plant and an exceptionally particular one.

**Ancient Distribution of Land.**—There are still evident some traces of the ancient divisions of the land areas of the world into a northern and southern mass, shown by the character of the vegetation. A good many families of plants are still confined respectively to the Northern and Southern Hemisphere. Thus many conifers, the pines, firs, etc., are distinctly northern types. The *Araucarias* and Kauri pine (*Agathis*) are equally characteristic southern coniferous types. Among the angiosperms, willows, oaks, birches, and maples are examples of families practically confined to the Northern Hemisphere. The very peculiar *Casuarina*, sometimes cultivated in California, and the *Proteaceæ*, of

which the silk-oak (*Grevillea*) is the best known, are examples of characteristic austral families.

**Floras of the Old and New World.**—The main elements of the north-temperate floras, of both the Old and the New World, are evidently derived from the Tertiary flora of the ancient northern continent, and many families and genera are still common to the Eurasian continent and North America. In the tropics, as we have already pointed out, the differences between the Old and New World are very marked. Probably the two richest botanical regions in the world are the Indo-Malayan region and tropical South America. A comparison of these two regions shows very few genera in common, and there are even many families which are peculiar to one region or the other. For instance, the palms of the Old and New World belong almost without exception to different genera, and the same is true of the vast majority of the orchids and other large families. The whole family of the Screw-pines is confined to the Old World, and the no less marked Pineapple family is peculiar to America. Where there are genera common to the tropics of both hemispheres, they are usually widespread ones, with representatives in the temperate zones between, and usually they are genera provided with very favorable means of distribution, such as certain *Compositæ* like *Vernonia* and *Senecio*. The great differences in the character of the floras of the two great tropical regions are easily understood, since these are

so very much isolated, and under the forcing conditions of the tropics, and the sharp struggle for existence, the change in species is presumably much more rapid than is the case in the temperate zones.

**Present Conditions in the Southern Hemisphere.**

—The conditions in the Southern Hemisphere, at present, are very different from those in the North. The Antarctic continent is an absolutely barren waste, with scarcely a vestige of any vegetation, and it is separated completely from the three principal land masses of the South—Australia, South America, and South Africa. While in the course of the ages which have elapsed since the three latter were united, the vegetation has become very much altered, there still are evidences of a common origin for the floras, although this is by no means so marked as in the Northern Hemisphere. The *Araucarias* of South America and Australia, and the *Proteaceæ* found in all three regions, are presumably descendants of the common primordial flora of the ancient southern continent.

**Floras of Isolated Regions.**—Wherever a region is shut off by barriers, either mountains, desert, or sea, the flora is certain to be very peculiar. In such isolated regions as the Cape region of Africa, Western Australia, or even regions like California or the shores of the Mediterranean, this is very evident. In all of these, climatic conditions are more or less similar and all of them have developed very rich and peculiar floras that show some interesting

analogies in the plants, although these may not be at all closely related. For example, both the Cape and California are characterized by a very large number of showy bulbous plants, but those in California are mostly of the Lily family, while in South Africa it is the Iris family which is especially developed. The cacti and century-plants of our Southwest are replaced in the drier parts of Africa by the leafless Euphorbias and Aloes, which superficially resemble to a remarkable degree the American cacti and agaves, but are not at all closely related to them botanically. It is probable that most of the existing plant types were pretty well differentiated in the later Tertiary and, as the fossil records show, the flora was fairly uniform over the Northern Hemisphere. At that period there is evidence that many existing genera, which are now restricted in their range, were widespread. In Europe, and even in Siberia and Greenland, there are found remains of such genera as *Sequoia*, *Taxodium*, *Liriodendron*, *Magnolia*, *Sassafras*; and laurels, and even palms abounded, all of which have long since vanished from these regions, but whose descendants still flourish in some more or less isolated regions, where they have survived the great readjustment of the flora, resulting from the Glacial epoch.

At the present day we may recognize a sub-polar zone, north and south temperate, and tropical zones, which of course are not absolutely defined. The

vegetation of the south polar zone is so scant as to practically amount to nothing.

**The Sub-polar Zone.**—In the sub-polar zone generally, much the same conditions, except temperature, prevail as were found during the pre-glacial epoch, and there is the same uniformity of vegetation, which, however, is much scantier, as might be expected from the more rigorous climatic conditions which now prevail. Throughout this area, from Northern Scotland and Scandinavia, to Eastern Canada, the same types give character to the vegetation. Poplars, willows, firs, and birches are the predominant trees, and in the meadows and bogs many beautiful flowering herbaceous plants give a charm to the brief summers of these high northern regions. Of course there are many plants in Canada and Alaska which do not occur in the Old World, but these are mostly emigrants from the South and may be said not properly to belong to the sub-polar zone.

**The North Temperate Zone.**—Proceeding southward from this uniform northern zone of vegetation, the increasing warmth causes a corresponding greater diversity in the vegetation, this diversity becoming more and more marked as the warmer tropical zones are approached. As the temperate zones of the Old and New World are now completely isolated, and have been so since the close of the Glacial epoch, a very much greater difference between the floras of the Old and New World is

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found than is the case in the northern regions. Even where common genera occur, there has been the development of new species, owing to climatic differences, and very few species are really common to these two regions except where these species also occur in the northern zone. Thus while Europe and Atlantic North America possess many genera in common, like the oaks, elms, walnuts, larches, asters, goldenrods, gentians, violets, etc., they are with few exceptions represented by quite distinct species. All of these may safely be considered to be the common descendants of Tertiary ancestors, which through isolation have become specifically distinct. On the other hand, there are numerous types which belong to one or the other of the two regions but are absent from the other. Thus Europe has no magnolias, tulip-trees, gums, sassafras, hickories, trilliums, milk-weeds, mandrakes, and very many more familiar American plants; while on the other hand, America possesses no daffodils, tulips, snowdrops, foxgloves, heaths, brooms, and many other beautiful flowers, which adorn the woods and meadows of the Old World.

Within the north temperate zone are enormous areas showing far greater differences of conditions than are found in the regions of the North, and in consequence their floras are far more varied. In the southern portions of this zone there is frequently an invasion of tropical types, and the limits between the temperate and tropical floras are very vague.

**The Tropics.**—With the approach to the tropics the northern types of vegetation gradually disappear, and are replaced by quite new ones. It is true that such northern types as pines and oaks may invade the tropics, but these are exceptional, and for the most part the plants of the hotter regions of the world are members of genera, and often of families, not represented at all in the colder parts of the world. The more intense growth conditions and the fierce struggle for existence result in a great diversity of plant-types adapted to all conditions of existence. It is in the tropics that one fully appreciates the possibilities of plant adaptation. Every tree in a tropical jungle is a veritable botanical garden, its trunk and branches covered with a mass of epiphytic growths, and giant creepers often overtop its highest branches. With this luxuriant growth there has developed an almost infinite variety of forms adapted to quite special conditions, and the differences between the plant types of the tropics of the Old and New Worlds are, as we have seen, far greater than is the case in the temperate zones.

It is only among the older and more conservative types of vegetation that the same or closely allied species occur. Thus while among the algæ, mosses, and ferns there are very many genera, or even species, that are common to the tropics of both hemispheres, among the flowering plants it is exceptional to find any genera in common, and where

they do occur, they are, as we have seen, genera which are widespread throughout the temperate regions. *Senecio*, *Vernonia*, *Acacia*, and *Ipomœa* are examples of some of these widespread genera. Among the characteristic tropical types, like the palms, aroids, bananas, etc., very few genera, even, are common to both hemispheres. Sometimes an Old World family is represented by an allied one in the tropics of the New World. Thus, for instance, the Ginger family is only found in the Old World, the *Canna* family in the new.

**The South Temperate Zone.**—The south temperate regions are very much more isolated than those of the north, and for the most part have very different types of vegetation, there being very little in common, for instance, between the flora of Argentina and that of South Africa. There are, however, certain similarities between the flora of the latter and some of the more temperate parts of Australia, and this is true also of some parts of South America, as, for example, the occurrence of *Proteaceæ* and *Araucaria*, which point to an ancient connection between these southern regions and denote that the flora of all of these regions have had a common, but very remote, origin. Unfortunately our knowledge of the fossils of the Southern Hemisphere is very incomplete, and for the present the geological history of the flora must remain unsatisfactory.

**Cretaceous and Tertiary Plants.**—There are

abundant plant remains from Cretaceous and Tertiary deposits throughout most of the Northern Hemisphere, which give a very good idea of the character of the vegetation of those periods. The fossils are largely impressions of leaves, mainly of trees and shrubs, the more delicate herbaceous vegetation having left no traces. The leaf impressions are often exceedingly perfect, and in many cases quite unmistakable, and it is evident from a study of these fossils that many modern genera were well represented. Oaks, poplars, willows, planes, common northern types of the present day, were common and widespread, and with these, very often in localities now quite unfitted for their growth, were genera belonging to warm climates, like the magnolias, palms, and laurels. The conclusion has been drawn that during the early Tertiary there was a fairly uniform flora throughout what is now the north temperate and sub-polar regions, but that the climate was much warmer than that now prevailing in the northern regions. While we have little knowledge from the fossil record of the herbaceous plants accompanying the trees and shrubs whose remains occur in Tertiary deposits, a study of the distribution of the living species gives us some clue as to what many of these probably were. Such widespread types as buttercups, anemones, violets, lilies, and many other familiar flowers, were in all probability represented by species not very different from their living descendants, and

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there were probably others which at present are restricted to limited areas, but which were more widely distributed during the Tertiary.

By the end of the Tertiary there was an evident lowering of the temperature, and the zonal climates were already well marked, but less pronounced than at present. Toward the end of the Tertiary the general distribution of the land areas was much as at present and the land connection between Europe and America was permanently severed. The end of the Tertiary was followed by the gradual formation of the great ice-sheet, inaugurating the Glacial epoch. The great climatic disturbances due to the development of the great polar ice-sheet, resulted in very marked changes in the distribution of the uniform northern Tertiary flora, and the advance of the ice-sheet was the principal factor in determining the distribution of the present flora of the Northern Hemisphere. With the increasing cold, and the southward extension of the great glaciers, vegetation of all kinds must have been forced southward. The result of this was very different in different parts of the world. In Europe, which lies mostly within the region of severe glaciation and whose great mountain ranges formed barriers against the southward retreat of the more tender plants, many plants were destroyed which have survived under the more favorable conditions presented in Eastern Asia and America.

It is evident from a study of European Cretaceous

and Tertiary fossils, that many genera once grew freely there, which are now quite extinct, but which have survived in America and Asia. Among these were cypresses, closely allied to our southern bald-cypress; Sequoias, related to the California big-trees, and redwoods; hickories, sassafras, tulip-trees, magnolias, gums, and other familiar denizens of our American forests. Some of these genera still survive in Eastern Asia, where conditions during the period of glaciation were quite like those in America, and where the present climatic conditions are also very much the same. In both Eastern Asia and America there is a continuous land extension southward, and the mountains run north and south, so that no barriers prevented the retreat of the vegetation before the encroaching glaciers, and the plants returned northward as the glaciers receded.

**Similarity in Floras of Eastern Asia and Eastern America.**—The great similarity in the general character of the floras of the Manchurian and Japanese regions, and to some extent that of China and the Himalayas, and that of Atlantic North America, is most marked. This is especially seen in the occurrence of certain small peculiar genera with no representatives in the intervening countries. This subject was one to which Professor Asa Gray gave much attention, and his work is of very great value and interest. He cites a long list of genera common to these two regions, but absent from the regions

between. Only a few cases can be given here, but these will be sufficient to illustrate the point. The very characteristic tulip-tree (*Liriodendron*) of Atlantic North America has an almost identically similar species occurring in China; the genus *Magnolia* belongs solely to Eastern Asia and Eastern America; *Wistaria*, *Stuartia*, *Ampelopsis*, *Hamamelis*, and many others show a like distribution. Many of these occur fossil, showing that they were once widespread, and that their present occurrence is a case of survival in widely separated regions where conditions happened to be favorable. While we know from the fossil records that these isolated types of trees and shrubs were once widespread, we can only conjecture that the same was true of certain plants whose distribution is now similar, but of which we have no fossil record. Among the most peculiar plants of Atlantic North America are certain herbaceous plants of the Barberry family. The mandrake (*Podophyllum*), and the twin-leaf (*Jeffersonia*), are examples of these isolated types. Each of these is represented in Eastern America by a single species, and the occurrence of another closely allied species in such remote regions as Japan and the Himalayas, makes it almost certain that these must be Tertiary genera once widespread, which have survived, just as the tulip-trees and magnolias have done in specially favored places. A long list of others might be cited, but one more must suffice. The beautiful trailing arbutus, or May-

flower, of our Eastern woods, has its mate in a second species growing in Japan, while elsewhere the genus is quite unknown.

As might be expected in the ages that have elapsed since the redistribution of the Tertiary flora took place, most of the forms have changed to some extent, so that it is rare to meet identical species in such widely separated regions as Japan and New England. The change has gone so far in some cases that a genus of one district is represented by a different but closely allied one in the other. Thus, for example, the flowering dogwood of Eastern America is represented in Japan by a closely allied genus, *Benthamia*. Identical species, however, may occur. The poison-ivy and the fox-grape of Atlantic North America are represented in Japan by what are usually considered to be identical species, and the sensitive-fern and the beautiful little orchid, *Pogonia*, are the same in Japan and Massachusetts.

Our knowledge of the geological history of the flora of the tropics is still incomplete, and as these regions were not influenced materially by the great Glacial epoch, and as the conditions in the tropical regions are conducive to rapid evolution of new forms, it is not remarkable that the tropical floras should differ very widely from the temperate ones. Moreover, as the tropics of the Old and New World must have been completely isolated from very remote times, migration from one to the other, ex-

cept in modern times, must have been so infrequent as to be practically of no account, and this explains the rarity even of generic types common to them. Except where these have been introduced by man, they are, as we have seen, genera which are widespread and generally occurring also in the temperate zones.

The development of the great continental areas in Asia and America caused pronounced changes in the climate, and the inner areas, arid and subjected to extremes of burning heat and arctic cold, could no longer support the moisture-loving plants which prevailed in pre-glacial times, and hence the restriction of these to the moister and more temperate regions nearer the coast. These arid plains also acted as a barrier against migration to the regions of the West, which were better adapted to their growth. In the United States, however, the Pacific coast, owing perhaps to its long dry summers, is not at present suited to the growth of many eastern trees, although we know that some of these once existed there.

**Influence of the Western Mountains upon the Climate of the United States.**—In the United States, the development of the great mountain masses of the West, must have exerted a great influence in determining the climate of the great central area, by shutting off the moisture-laden winds of the Pacific. The Rocky Mountains were formed at the end of the Cretaceous,

and presumably the region immediately to the east of the mountains then, as now, was one of slight rainfall. In a recent, very interesting study of the prairie flora, Harvey has given a very plausible explanation of the divergencies of the western and eastern floras within the United States. He holds that even during the Tertiary the great plains region was too dry for the growth of forests. With the retreat of the northern forests before the advancing glaciers, these prairie regions, unfitted for forest growth, acted as a wedge, one company of migrants working to the westward, and characterized by the predominance of coniferous trees; the other flowing eastward, and typically deciduous, followed the Mississippi and its tributaries and became settled in the Appalachian region of North Carolina and Tennessee, where to-day it forms the finest deciduous forests in our country.

#### ALPINE PLANTS

Very interesting is the survival of many northern plants on high mountains, often very remote from each other. It is supposed that these northern plants, driven southward by the increasing cold, retreated up to the cooler regions of the higher altitudes as the climate became warmer, after the retreat of the glaciers. Even in the tropics, close to the equator, one meets on the tops of high mountains a real northern flora, including such familiar

types as buttercups, strawberries, violets, brambles, primroses, gentians, and others obviously of northern origin, and quite unrelated to any of the plants of the adjacent lowlands. These isolated waifs, in the course of ages, and under the milder conditions prevailing, even on the high mountains in the tropics, have become specifically changed, but have nevertheless retained their generic characters.

Some of the high, isolated peaks of the tropics afford striking instances of the change in vegetation due to altitude. The great volcanic mass of the Gedeh in Western Java, is an especially good example of this. This mountain rises to a height of 10,000 feet, and lies but a few degrees from the equator in a region of very heavy rainfall. As one ascends from the luxuriant tropical vegetation of the lowlands at the base of the mountain, a change is very soon apparent. At about 4,500 feet (1,400 m.) the temperature has fallen many degrees, and although the heavy rains and almost constant clouds and mist promote an extraordinarily luxuriant forest growth, many of the strictly tropical types like palms and bamboos have nearly disappeared, and a number of northern types become common. Oaks, chestnuts, and maples occur, and several trees belonging to genera common in our Southeastern States are met with. The loftiest tree of this mountain forest (*Altingia excelsa*) is related to the sweet gum (*Liquidambar*) of the Eastern United States; and species of *Nyssa*, like the pepperidge or "sour

gum," of Eastern America, also occur, and one of the showiest of the smaller trees, *Gordonia*, with big white flowers like Cherokee roses, belongs to the same genus as the loblolly bay of the Gulf States.

The northern aspect of the vegetation increases rapidly as the summit of the mountain is approached. The low, gnarled trees composing the forest are bearded with gray lichens, like those of the northern forests, but from these same trees hang beautiful orchids, not at all reminiscent of the North, and the stately tree-ferns, as well as many other plants unfamiliar to the northern botanist, remind him that he is still in the tropics, in spite of the cold gray skies. At this altitude a number of showy small trees and shrubs of northern origin are common. Huckleberries, wintergreen (*Gaultheria*), and fine orange and scarlet rhododendrons are common. Thickets of brambles, and carpets of everlastings (*Gnaphalium*), buttercups, violets, balsams, and other familiar flowers abound, and in the sheltered thickets among the bushes are colonies of a stately primrose, *Primula imperialis*, which for many years was known only from this mountain. Many of these plants, like the primrose, have their nearest relatives in the Himalayas, and it has been suggested that the seeds of some of them may have been carried by the strong, prevailing winds of the upper atmosphere, which blow southeastward for long periods. This, however, seems hardly probable in the case of many of the species, whose presence

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on this isolated mountain top is better explained on the theory of migration due to the Glacial epoch.

The Alpine plants of the temperate regions may be specifically the same as species growing at sea-level in higher latitudes. On the higher summits of the New England mountains and the southern Alleghanies, one sees tufts of the pretty little Greenland sandwort (*Arenaria grænlandica*), which is unknown in the neighboring lowlands, but flourishes at sea-level in Labrador and Greenland; and in the higher regions of the Rocky Mountains as far west as Utah, a beautiful little flower, *Dryas octopetala*, one of the most characteristic of arctic flowers, is a common and conspicuous species. This species is also abundant upon the mountain summits of Europe.

### ISLAND FLORAS

Remote islands afford some interesting problems in the evolution of new species. The more remote the island, the less likely that new forms will be brought to its shores, and the more probable that the forms which do so will have time to change, in accordance with the new conditions to which they are subjected. Perhaps the most striking case known is that of the Hawaiian Islands. These are volcanic masses, thrown up from great depths, and separated by long distances from any other land. The islands are of different ages, and evolutionary

forces have been at work longer in some of them than in others, and it can be clearly seen that this longer time has been efficient in producing a more varied and specialized flora in the older islands.

Thus the island of Kauai, the oldest of the group, has many more peculiar species than the very much larger but more recent island Hawaii, which is still in process of formation. The flora of these islands is derived mainly from the Polynesian region to the south, but there are also evidences of some American immigrants. Most of these, however, have become so changed, that of the certainly indigenous species of vascular plants, it has been claimed that over eighty per cent are endemic, i.e., are peculiar to the islands, a proportion probably unequaled in any other region of the world, except perhaps in the very isolated area of Western Australia.

**The Flora of Krakatau.**—The reestablishment of the vegetation upon the island of Krakatau is an instructive demonstration of the origin of island floras. In 1883, this volcanic island lying in the Straits of Sunda, between Java and Sumatra, was the scene of the most violent volcanic disturbance that has ever been recorded. The greater part of the island was blown into space by the great explosion, and what was left, as well as some of the neighboring islands, was covered deep with hot cinders, which completely destroyed all vegetation and left the island a barren desert.

A visit was made to the island three years later,

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and by that time a good many plants had already established themselves. Apparently the earliest plants to get a foothold were blue-green algæ, which were found growing on the barren cinders, forming black gelatinous films in which fern spores were able to germinate, so that nearly a dozen species of ferns were noted on this first visit.

With the rapid decay of the dead vegetation, and the decomposition of the ashes under the sun and rain of an equatorial climate, soil enough was soon created for the maintenance of many flowering plants, whose seeds, borne by the wind, or by birds, or carried by the ocean currents to the shore, quickly spread over the bare surface of the island.

I had an opportunity of visiting Krakatau in April, 1906, twenty-three years after the eruption. At this time the island was completely covered again with vegetation comprising a large number of species of flowering plants. Along the shore, the characteristic strand flora was completely reestablished. Fruiting cocoanut palms, Casuarinas, screw-pines, and various other trees, some of them fifty feet in height, formed a belt of forest, with lower vegetation growing immediately along the beach. The flat land between the shore and the remains of the cone in the center of the island, was covered with a dense growth of tall grasses, with a sparse growth of shrubs and other plants between. In the more sheltered hollows about the base of the cone, a dense growth of young forest trees had established itself,

and probably in time will extend itself to meet the forest belt near the shore.

Professor Ernst, who accompanied the party in 1906, has since published a full account of the flora as it was noted at the time of this visit. ("The New Flora of Krakatau," by A. Ernst: Cambridge University Press, 1909.)

### THE AGENTS IN PLANT DISTRIBUTION

**Man as an Agent in Plant Distribution.**—The agents in plant distribution are many. Wind and water may be the vehicles of transportation, and many animals, especially birds, are often the agents of rapid dissemination of many seeds and fruits which are often provided with special organs facilitating their distribution. With the rapid spread of man into the remoter parts of the earth, many plants have been carried with him, intentionally or otherwise, and these have often very quickly made themselves at home, and sometimes have driven out their native competitors, very much as the white man has driven out the less fit savage. The rapid spread of these imported plants often gives quite a different aspect to the region which they have invaded from what it had before, and may disguise the essential differences which existed between it and other regions. It is often very hard to trace the origin of some of these imported plants, and the task of the student of plant geography is greatly increased by

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the presence of these imported plants in nearly every part of the world. Few persons would imagine that the daisies, dandelions, and buttercups, which spangle the meadows and lawns of our Eastern States are probably all of them European immigrants, and that the thistles and burdocks along the roadsides are likewise aliens. Railways and ships spread the seeds everywhere, and when the conditions are favorable, the newcomers quickly adjust themselves to their new home.

**Barriers to Plant Distribution.**—The great natural barriers to plant migration are deserts and high mountains, and large bodies of water, like the oceans. The presence of over a thousand miles of desert and mountains between the Mississippi and the Pacific Coast largely explains the striking differences in the vegetation of California and that of the Atlantic States.

While mountains are the barriers which prevent the passage of many plants, they may also be highways along which plants travel. Thus the great ranges of mountains running north and south, permit the southward migration of northern plants, and the northern migration of antarctic ones. Ascending higher and higher as they go southward, many arctic or north temperate plants have established themselves on the mountains far southward of their original habitat.

## PLANT DISTRIBUTION IN THE UNITED STATES

The North American continent illustrates very clearly the most important factors governing plant distribution, and the United States with its 3,000,000 miles of territory, reaching from the Atlantic to the Pacific, offers unusual opportunities for studying the most important factors of Phytogeography.

**The Eastern Forest.**—In a general way the United States may be divided into three great regions, extending east and west. East of the Mississippi the country was originally covered by an almost unbroken forest, of which a very large part has disappeared with the clearing of the land, but enough of which remains even in the more densely settled regions, to make it evident what was its character; and in the remoter districts, especially in the southern mountains, there may still be found tracts of practically virgin forest. This forest is characterized by the predominance of deciduous trees, only occasionally, as in the pine-barrens and cypress-swamps of the South, or in the more northern forests, are conifers the predominant trees.

Owing to the absence of high mountains, or other barriers, the flora of the eastern third of the United States is remarkably uniform, many species occupying the whole area, the differences in the different portions being mainly those caused by variations in soil, heat, or moisture. In the northern portion the prevailing trees are oaks, elms, maples, hickories,

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etc., with a mixture in places of pines, firs, hemlocks, and some other conifers. Its general character approximates that of northern Europe, and it merges into the still more uniform forest flora of the sub-polar zone to the North. But even in the more northerly territory of the Eastern United States, types occur which are quite absent from the European flora. Hickories, walnuts, and sassafras are extra-European genera which exist in Canada, and somewhat further south other peculiar forms, magnolias, tulip-trees, persimmons, gums, locusts, and other less familiar types, absent from the European forests, add variety to the magnificent forest which reaches its finest development on the slopes of the Southern Appalachian mountains. In the southernmost parts, e.g., Southern Florida, a strong tropical element derived from the neighboring West Indian flora is conspicuous. This includes such forms as the palms, mahogany, and wild pineapples. Some tropical types have even made their way far north. Thus the pawpaw, a member of the tropical family of Custard-apples, occurs as far north as Southern Michigan. Besides the trees, there are many beautiful shrubs and herbs that characterize these splendid forests. Before the leaves appear in the spring, many delicate herbaceous plants, blood-root, Dicentra, spring beauties, dog-tooth violets, anemones, trilliums, etc., rapidly spring up, expand their flowers, and as quickly disappear, to rest until the next spring. Many flowering shrubs

adorn the woods, azalea, and rhododendron, syringa, honeysuckle, crab-apples and hawthorn, dogwood and redbud; and especially in the southern woods, beautiful creepers, grape-vines, clematis, wistaria, bitter-sweet, yellow jasmines, trumpet-creepers, and passion-flowers, and others, remind one of the lianas of the tropics. Only in the extreme South do we encounter palms, perhaps the most striking tree types of the tropics.

Passing inland from the Atlantic coast there is a marked diminution of the rainfall, accompanied by a corresponding falling off in the forest flora. In Western Michigan, Indiana, and Illinois the forest assumes a more open character, and shows much less variety in the trees. Oaks predominate, and these "oak openings" are very characteristic of the territory abutting on the prairie region lying to the west, and small prairies already appear in spots between the forested areas. These patches of forest finally disappear entirely, and the great plains extending from the Mississippi to the Rocky Mountains are quite treeless, except along the streams, where a belt of cottonwoods or willows often marks the course of some shallow muddy river.

**The Great Plains.**—The great plains constitute the second phytogeographical region. A level or slightly rolling plain, with meager rainfall and great extremes of heat and cold, and with fierce winds sweeping it, the conditions are not favorable for

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plant growth, and only particularly hardy plants can survive. First in importance are the grasses, which cover the entire eastern portion with a close turf, but among these there also grow many beautiful flowers which in spring and summer dot the prairie with spots of vivid color. Only along the water courses, or in sheltered gullies, can trees find a foothold. The soil of these eastern prairies is extremely fertile, and now they are the granary of the whole country, immense fields of corn and wheat covering the plains which a generation ago were unbroken prairie sod. With the rapidly diminishing rainfall westward, the close turf of the eastern prairies gives place to arid expanses, dotted with bunch-grasses mingled with low cacti, sage-brush, and other outposts of the true desert lying still further west. These arid plains which have risen very gradually, end abruptly in many places, the Rocky Mountains rising steeply from the plain and forming the beginning of the great complex of mountain and desert which reaches from the great plains to the Pacific.

**The Western Flora.**—This western third of the continent is in many ways the most interesting of all to the botanist, as it presents a far greater variety of conditions than prevails in the eastern half of the continent. For the most part it is a region of light rainfall, and much of it is a true desert where such plants as can survive are extremely modified. Some mountain valleys are well watered,

however, and the beautiful glacial parks of the Rocky Mountains, adorned with luxuriant meadows and fine forests, present a great contrast to the barren deserts of Arizona and Nevada. Except in a few places these deserts support a scanty, but extremely characteristic flora, which has adapted itself to the rather strenuous conditions of desert life. Especially interesting are the desert forms of the Southwest. Here the cacti, Yucca, century-plants, and many other striking desert types are especially well developed, and in some of the canyons opening into the hot sandy waste of the Colorado desert in Southern California, are groves of lofty palms that might have been transported bodily from the tropics.

**The Pacific Slope.**—The Pacific coast forms almost a distinct botanical region of its own. Shut off from the country to the east by the great barrier of the Cascades and the Sierra Nevada, it shows many peculiarities in its flora, these being particularly marked in California, where the isolation is practically complete. This great mountain barrier exercises a profound influence on the climate of the Pacific coast, which is dominated by winds blowing from the Pacific, the temperature of which varies but little, so that it acts as a great thermostat. Instead of the sudden changes characteristic of the continental climate of most of the United States, the Pacific coast has a climate which is remarkably uniform. The difference between the mean

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of the hottest and coldest months in San Francisco is only  $10^{\circ}$  F., while in Washington, with nearly the same latitude, and with the same mean annual temperature ( $55^{\circ}$ ), it is  $44^{\circ}$ . The rainfall is very heavy at the north, but rapidly diminishes towards the south, so that San Diego, in Southern California, receives only about one-tenth as much rain as falls at some points on the northern coast. The rain falls mainly in the winter and spring, the summer being almost absolutely rainless. These very great differences in climate, compared to Atlantic North America with its cold winters and wet hot summers, result in a remarkable difference in the type of vegetation. Moreover, in addition to the great differences in rainfall in different parts, there must be considered the differences in altitude, which in California approach 15,000 feet, involving of course very great variation in temperature and exposure. Consequently in proceeding down the coast of California from Humboldt and Mendocino Counties, to the Colorado desert of the southeast, one passes from forests of enormous trees with an almost tropical luxuriance of undergrowth, to barren deserts where no plant can live. The mild climate induces a growth of evergreen plants, even deciduous trees and shrubs retaining their foliage for the greater part of the year.

All through the West there is a predominance of coniferous trees, this being especially the case in California, where most of the forests are com-

posed of pines, firs, redwoods, cedars, etc. The deciduous trees, like the oaks and maples, form, as the rule, only the undergrowth for the much taller conifers, except along the streams, and sometimes in the mountain canyons, where often the growth is mainly of deciduous trees. Many of the angiospermous trees, however, are also evergreens, like the live-oaks, tanbark-oaks, madroño, and laurels, and a very characteristic feature of the drier formations in California is the dense scrub, or "chaparral," composed of a great variety of shrubs, most of them evergreens, like the manzanita and toyon, but with some deciduous species like the buckeye and poison-oak.

**The Flora of California.**—California illustrates very perfectly how important a part topography plays in the origin of a flora. The Sierra Nevada and Coast Ranges form perfect highways for the migration of northern plants, which follow the mountains southward, ascending as they go to the altitude best fitted for them. In the cool moist forests of the outer Coast Range the northern types are especially at home, and many of the common flowers, violets, trilliums, spring-beauties, dog-tooth-violets, Solomon's seal, etc., are closely related to species that are common in the Eastern and Northern United States. With these are a few forms like the fritillaries and western skunk-cabbage, and the Sitka-spruce, which seem to be immigrants from the Old World, *via* Alaska.

The majority of the Californian plants, however, the flora of the drier mountains and valleys, is of Mexican affinity, and the many showy flowers like the poppies, cream cups, lupins, nemophila, *Gilia*, *Orthocarpus*, and Mariposa-lilies, and many others which make so splendid a showing in the open valleys and upon the hillsides of California in the spring, are for the most part very different from any Eastern flowers and belong to the flora of the great Mexican plateau, of which Arizona and Southern California are really a part. In Central California the two floral regions meet, the northern types of the Coast Range often following the stream-beds down into the valleys, and between the hills, where the southern flora predominates.

As in other settled countries, the character of the flora has been modified by man to a great extent. California, however, being largely an open country, has not had its flora so much altered as was the case in the forested Eastern States. It is true that the forests have been to some extent cut, but more for timber than for clearing the land, the cultivated areas being mainly open country. Cultivation, however, has resulted in the introduction of very many foreign plants, and by irrigation the desert has been transformed into rich fields of alfalfa, or into orange groves and vineyards. With the vines and olives of the early settlers, came in also many weeds, bur-clover, wild-oats, and mustard, which found

themselves very much at home in the fields of California, where they contested the ground with the native poppies, buttercups, and lupins, which, however, manage to hold their own pretty well against the invaders.

## CHAPTER IX

### THE HUMAN FACTOR IN PLANT EVOLUTION

**T**HE changes in the vegetation of the earth due to the direct or indirect agency of man have been great and far-reaching. Like all other animals, the very existence of man is dependent upon plants of some kind, and most races of mankind rely upon some single species of plant as the staff of life. While the Eskimos of the frozen North, and the nomad tribes of Indians of the western plains, depend mainly upon the products of hunting and fishing for their existence, by far the larger part of mankind are vegetarians in their diet, animal food playing a quite secondary rôle. If the original home of man was in the eastern tropics, as there seems every reason to believe was the case, his natural food would probably have been mainly fruits, seeds, and roots. Such shelter as was necessary for him was furnished by bunches of branches or leaves, or mud huts thatched with grass or palm-leaves, such as we now find among many of the lower savage tribes. Even at the present day, wild plants yield a not unimportant source of food for mankind.

Wild fruits, like the nuts and berries of temperate climes, are by no means despised even by the most civilized peoples, and the savages of the more prolific tropical zones depend very largely for their subsistence upon the fruits and roots growing spontaneously in the forest. Man also, at a very low stage in his development, learned to use the tenacious fibers of many wild plants for clothing and for other purposes. In its most primitive form this still survives in the "tapa" or bark cloth of the South Sea Islanders. Spinning and weaving were much later achievements. A few wild fiber plants are still of some commercial value, the most important of these probably being the wild flax (*Phormium tenax*) of New Zealand, which is manufactured in considerable quantities, and forms an important article of export.

As primitive man migrated from the fertile tropical forests, where he had his birth, to regions less prolific in wild food plants, he was probably driven to feeding on a much greater variety of food than was his early habit, and we may assume that his more marked carnivorous tastes were gradually developed. At the present day there are savage tribes whose food supply must be quite as precarious as that of their ancient forebears. The inhabitants of the far North and the South, or such degraded savages as the native Australians, eat pretty nearly anything which they can procure, and in times of scarcity are often driven to feed upon most un-

wholesome plants. Some of the native Californian Indians still collect acorns, pine-nuts, and such other wild seeds and berries as they can gather, with grasshoppers, caterpillars, and other similar small game for variety.

Such wild fruits as the strawberry, huckleberry, cranberry, persimmon, nuts, etc., are much esteemed by everybody, but can hardly be considered as important articles of diet. Among the savage tribes, however, these wild fruits and seeds may be the staple sources of their food supply. The Indians of the Great Lake region used regularly to harvest the wild rice, and the Californian Indians looked upon the oaks and nut-pines as their harvest fields. The South Sea Islander gathers cocoanuts or bread-fruit, and most savages depend to a greater or less extent upon the spontaneous products of a more or less generous nature.

In the tropics especially, it is hard to draw the line between cultivated and wild plants, as so many of the cultivated fruits, like oranges, mangoes, and bananas, readily escape from cultivation and are often found growing far from any cultivated ground, offering their fruits to whoever may care to gather them.

**Origin of Agriculture.**—The development of agriculture must have been very gradual and largely a matter of chance. It is more than probable that even in the earliest stages of agriculture and horticulture, there appeared quite accidentally varieties of

fruits or grains which were sufficiently superior to the common wild forms to attract the attention of the primitive husbandman, who would naturally prefer these, and at the same time may have taken the trouble to plant the seeds of these superior forms, thus inaugurating a most important epoch in the history of mankind, since the development of agriculture made it possible for man to spread to regions which without cultivation would have been unable to support him.

Succeeding the more or less casual planting about his dwelling of wild fruit-trees, it may be surmised that primitive man began to follow methods of agriculture approximating some of those in vogue among savage races at the present day, and indeed not entirely unknown to the white man. The native of the tropics—and of the Southern Alleghanies—still girdles the trees so as to make a clearing in the forest, and plants his crops in the space thus opened to the sunlight. After a few crops have been taken off from this clearing, it is deserted and another one made. Nature promptly repairs the damage, and another generation sees the forest again in possession.

The extension of agriculture to more arid regions necessitated more careful methods, and it was especially in such regions that the most scientific methods of agriculture, including irrigation, had their birth, and thus were made possible the civilizations of Babylonia and Egypt, Mexico and Peru.

**Antiquity of Certain Cultivated Plants.**—As far back as history runs we encounter evidences of the cultivation of many food and textile plants still in use. This is true in Egypt, China, and India, and in the New World the advanced civilization shown by remains of man in Peru and Mexico, show that agriculture had reached a high degree of perfection at a very remote period. Among the most interesting evidences as to the early cultivation of many useful plants in prehistoric times, are the remains of the Swiss Lake-dwellers. At a period when these ancient people still used only stone implements, they cultivated a variety of food plants, including wheat, barley, and millet, and they also grew flax.

First in importance among cultivated plants are those grown for food, and among these the various grains take first place, followed by certain fruits; but other parts of the plants—the leaves, roots, or tubers—may also be important sources of food. Next in importance are plants furnishing fibers, usually derived from stems or leaves, the most important exception being cotton, which furnishes a fiber attached to the seed. Some of these fiber plants, especially flax and hemp, have been cultivated from the earliest historical times, but the history of some of the less familiar fibers, like jute, Manila hemp, and ramie, is very imperfectly known.

It is probable that very early in his history, man learned the virtues of certain medicinal plants. In his search for food plants he doubtless, through

more or less unpleasant experience, discovered the narcotic properties of opium and tobacco, the stimulating effects of tea and coffee, the cathartic qualities of various seeds and barks. While medicinal plants must be considered of much less importance than the staple food plants, still they are in many cases of very great value, as for instance quinine, which has made it possible for white men to live in certain fever-stricken regions in the tropics where otherwise they could not have existed.

The last category of useful plants comprises those grown for constructive purposes, like timber trees and bamboo, but even at the present day the supply of timber is largely drawn from natural forests—tree planting for timber being a recent development, but one of rapidly growing importance and likely to affect strongly the character of large tracts of country in the United States and elsewhere. . . .

Just when the first attempts at agriculture were made is not known, but it is evident from historical record that in all the ancient civilizations of which we have any trace, many plants were regularly cultivated. Thus in ancient Egypt wheat and flax were grown, and in China, 5,000 years ago, there is evidence that rice, wheat, sweet potatoes, and millet were cultivated. In America, long before its discovery by Europeans, Indian corn, potatoes, and tobacco, and other plants were regularly grown, but very little is known of the exact age of these early civilizations in South America and Mexico.

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All but the lowest savages and certain nomad races cultivate some forms of plants for food, but in many cases these have been cultivated from the earliest historic times and have become so altered by cultivation that their origin is a matter of very great uncertainty.

It is in the improvement and subsequent changes of the food plants that man's influence as a creator of new plant forms is most clearly seen. The development of new ornamental plants, except in very recent years, has been relatively unimportant, and practically all of these are clearly traceable to wild ancestors which still exist. Many wild fruits like strawberries, raspberries, crab-apples, etc., have been brought under cultivation but have been altered comparatively little. In some of these cultivated forms it is evident that two or more species have been crossed, and this sometimes makes it difficult to be quite certain as to their origin. Many tropical fruits, such as the mango, mangosteen, cocoanut, durian, custard-apple, and many others, are good botanical species, existing but little changed in the wild state. None of these, however, can be looked upon as the main source of food supply, and perhaps this accounts for the comparatively slight changes that they have undergone in cultivation. The various fiber plants, like flax, hemp, and cotton, have been but little altered, since the flowers and fruit do not influence in any way the character of the fiber. It is evident that prehistoric man utilized the fiber

of many plants, first probably for fish-lines and for binding the heads of arrows and spears and axe-heads to the shafts, etc., but he later learned the art of spinning and weaving, to provide himself with clothing. The ancient Egyptians knew the art of weaving, and, as we have seen, there is evidence that even the Swiss Lake-dwellers cultivated a species of flax.

**Forage Plants.**—Besides the plants used directly by man for food, there must be taken into account the forage plants, which serve to nourish the animals upon which man feeds. These, like the staple food plants of mankind, are largely grasses, most of the herbivorous animals, like cattle, sheep, etc., feeding largely upon grasses of various kinds. Next in importance as forage plants are various leguminous plants, clover, alfalfa, etc. These have become little altered by cultivation and to all intents and purposes are still wild plants.

**Cereals.**—The food staple of nearly all peoples is some form of farinaceous vegetable food, and this is seen in its greatest perfection in the grains yielded by various species of grasses, which from very early times have formed the principal food for the vast bulk of mankind. Some of these grains have been in cultivation as far back as there is any historical record, and indeed, as we have seen, there are evidences of the cultivation of grains even in prehistoric times, as shown by remains of the Swiss Lake-dwellers of the stone age. In consequence of

the enormously long period during which these have been under cultivation, they have lost most of their original characters, and it is almost impossible to determine what their progenitors were, and whether they still exist in the wild state. It has been argued from the rapidity with which plants are known to change under cultivation, that the ancestors of some of the cultivated grains may still exist in the wild state, but so different from their cultivated descendants as not to be recognizable. The most important of these grains are wheat, rice, and maize.

There is much doubt as to the origin of the different cultivated forms of wheat, and it is still a question whether they really all belong to a single species. Probably they were derived from some species inhabiting the region of the Euphrates, and perhaps also parts of Southeastern Europe, but just exactly what these species were, is by no means clear. Rice has been cultivated from the earliest historic times in India and China, and wild rice apparently specifically identical with the cultivated plant still grows in India. It might be said here that the "wild rice" of the Eastern United States, which was so important an article of food among certain of the North American Indians, is an entirely different plant from the Oriental rice. Maize, the staple grain of the New World, has been cultivated from the earliest times of which there are any records, both in Mexico and South America. It is

unknown in the wild condition, but there are certain grasses related to maize which it has been surmised may possibly be the wild plants from which the cultivated maize has arisen.

**Fruits.**—In some countries grains are replaced to a great extent by fruits like the banana and breadfruit, or tubers like the taro or the potato. The banana in its many forms has been cultivated from the earliest times in the Asiatic tropics, and Humboldt states that it was cultivated in America prior to its discovery by Columbus; but this seems to be very doubtful, as all wild bananas are Asiatic and it seems practically certain that the banana was introduced into America shortly after its discovery by Europeans. As the cultivated bananas are seedless, their spread into foreign countries is absolutely dependent upon human agency. The same is true of the breadfruit, which has been carried from its home in Java to all of the moister regions of the tropics. It is quite common to find the breadfruit and banana growing far away from human habitations, and this is true also of the taro, which is known in the wild state in the warmer parts of the Indo-Malayan regions. It has been carried by the Polynesians to all the warmer parts of the South Seas, and is still a very important article of diet among the Hawaiians. The potato was cultivated in America, especially in the mountain regions of South America, long before the advent of the Europeans.

It still exists in the wild state in Chili and possibly in the mountainous regions to the north.

### **Man's Spread over the Earth Due to Agriculture.**

—With the adoption of agricultural habits, the possibilities of man's expansion over very wide areas of the earth's surface became possible, and as a result of his migrations the vegetation of the invaded regions has been very greatly altered. The clearing of large tracts for agricultural purposes, and the replacement of native plants by cultivated ones, has very much changed the aspect of great areas of the earth's surface all over the world. Little of Europe is in a state of nature, and the same is true of southern and eastern Asia and northern Africa. In the old settled countries, like most of Europe and much of Asia, all traces of the original forest have long ago disappeared, and one must go to the most remote mountain regions to find any remains of it.

In the tropical regions the jungle quickly grows up again when cultivation is neglected, but this is not the case in the colder and drier climates of most parts of Europe. In the United States, the greater part of the dense forest of the Atlantic region has given way to great cities, or to fields, meadows, and orchards largely occupied by alien plants—wheat, corn, clover, and fruit trees, of various kinds, and all the familiar garden flowers and vegetables. These are, with very few exceptions, foreigners, which have replaced the native forest trees and undergrowth. Moreover, with these introduced, culti-

vated plants have crowded in hordes of less welcome immigrants, the troops of foreign weeds which have taken possession of all the waste places along the roadsides, fence corners, and other places not monopolized by the crops. Most of the more aggressive weeds, thistles, dandelions, burdocks, sorrel, etc., are of European origin, these hardy invaders ousting the delicate shade-loving native plants which thrive only in the shelter of the dense forest. Only in the swamps and other similar open places do the native plants hold their own against the foreign invaders. . . .

**Introduced Plants.**—It not infrequently happens that plants escape from cultivation and find themselves so much at home that they have all the appearances of natives, and this has led to many errors in determining the origin of many cultivated species. Thus the orange grows spontaneously in the forests in Florida and Jamaica, and is to all appearances wild, but we know that it is a native of the Old World and was unknown in America before the advent of the Spaniards. The banana also is often met with in the forests of nearly all tropical countries, but there is no question that it is an escape from cultivation, and the same is true undoubtedly of many other tropical fruits, like the mango and guava. The readiness with which cultivated plants adapt themselves to their new homes, makes the discovery of their real origin often a matter of very great difficulty.

In the case of primitive man, especially in the tropics, the effects of cultivation were probably insignificant. A few acres of forest burned off, or the trees girdled and left to die, furnished the crude field where he planted his crop of yams and corn, and after a few crops had been taken off, the plot was left to revert to forest. Very different has been the case in modern times, where man has spread over the whole world, and profoundly changed the character of the vegetation of vast areas of the earth's surface. These changes have been going on steadily in many parts of the Old World for many centuries, but it is in the more recently settled regions, like the United States and Australia, that the great changes in the vegetation due to the invasion of man can be best appreciated. Perhaps the United States, more than any other country, will illustrate this most vividly, owing to the great rapidity with which it has been settled during the past century.

**Changes in America Due to Cultivation.**—A hundred years ago, all but a small part of the Atlantic third of the United States was an almost unbroken forest, with very little open land except marshes and swamps, and in the western parts, the small prairies, which were the outposts of the great plains of the trans-Mississippi region. Aside from the trees, the undergrowth consisted of shrubs and herbs fitted for the most part to growth in the dense shade of the forest, and quite unadapted to

survive the clearing away of the forest cover. Before the ax of the pioneer these forests rapidly disappeared, and the clearings were planted with the crops upon which he depended for food, or were allowed to run to grass for the subsistence of his herds and flocks. In these clearings the delicate plants of the shady forest perished, and the waste places were gradually invaded by hordes of foreign weeds, brought in the seed, or carried on the coats of the stock or in the belongings of the immigrant. These hardy foreigners have now so established themselves that any one but the botanist takes for granted that they are natives. Few people realize that the majority of our familiar weeds, the dandelions, daisies, buttercups, etc., are European immigrants. These in many cases have proved themselves so well fitted to their new home, that they have almost monopolized the waste places, and have invaded the cultivated lands, so that they have become pestilent weeds. It is hard to realize that little more than 300 years ago there were none of these common weeds to be met with in America. With the rapid extension of the settlement of the western plains, due to the opening up of railroads, which offered rapid transit for man and also for weeds, very new conditions were met with. The exposed prairie was the home of many hardy plants fitted to live in the open, and many of these prairie weeds—sunflowers, yellow ox-eye daisies, ragweed, and many others, migrated eastward and joined the

army of European weeds, with which they managed to compete pretty successfully, and now mingle with them on an equal footing in the floral display of the meadows and roadsides of the New England States.

Sometimes plants that have been introduced for ornament or for useful purposes, prove so well adapted to their new home that they escape from cultivation, and may become a veritable pest, just as in the animal kingdom the rabbits in Australia, and the sparrows in America, have proved altogether too well fitted to their new homes. A good instance of this is found in the Hawaiian Islands, where a rather pretty garden shrub, Lantana, has spread over all the drier lowlands so that it now has become a real nuisance. It is said that the Mina, a bird introduced from India, is largely responsible for distributing the seeds of the Lantana. In New Zealand, the sweet-briar and gorse, introduced by the early British settlers, have similarly escaped from cultivation and become troublesome weeds, and many similar cases can be cited from various parts of the world.

**Deserted Land Returning to Forest.**—As the arable lands of the East have been exhausted, and deserted for the rich prairie farms of the Middle West, they have often been abandoned, and now Nature is trying to repair to some extent the ravages made by man. Many of the deserted farms in New England and New York have rapidly reverted

to forest, and vigorous growths of the same trees—pines, oaks, maples, and walnuts—that once covered the whole region with an unbroken forest, are again taking possession of the soil which for a hundred years or more was devoted to agriculture.

**Effects of Clearing the Forest.**—The clearing of the country has also affected the vegetation in another way. By the removal of the forest cover, especially in the mountainous regions, there has often resulted a disastrous denudation of the soil, due to the washing of heavy rains, and to landslides. The washing away of the fertile surface soil makes it impossible for many plants, which formerly occupied these places, to grow, and the bare slopes can only support species which are fitted to live in an impoverished soil. The drying up of the lowlands, due also to the interference with the water supply, the result from the clearing off of the forest, must necessarily affect very strongly the vegetation of the region. There is little evidence that the total amount of rain in a forested region is materially diminished by clearing the land; but the effect upon the flow of springs and streams is very marked. On a forested mountain side the shade of the trees checks the evaporation from the soil, and the undergrowth and spongy masses of decaying leaves and twigs allow the water to percolate slowly through, reaching the sources of the springs and streams gradually and keeping the flow steady. When the land is cleared, the water runs off quickly, making the

streams raging torrents after heavy rainfalls and when the snow melts, only to leave them shrunk into insignificance in the heat of summer. This disturbance of the water distribution necessarily affects very strongly the vegetation of the region concerned. Of perhaps as much interest scientifically as practically, is the result of extensively reclaiming swamp areas. The swamps and bogs are the haunts of many of the rarest and most beautiful of our native plants, which have taken refuge in these inaccessible sanctuaries. The tamarack swamp, with its beds of peat-mosses and dense undergrowth, was the happy hunting ground of the botanist. Now with the draining of the bogs, there are rapidly disappearing many of our loveliest orchids, the cardinal flower, pitcher-plants, and hosts of other curious and beautiful botanical treasures.

**Introduction of Foreign Plants.**—The widespread introduction of ornamental trees and garden flowers into civilized countries has also much changed the appearance of the vegetation in all of them. In any long-settled community it is astonishing how little of the vegetation which one encounters is really native to it, or if so, has not been planted by man. Indeed at present, if one wishes to see the unchanged indigenous vegetation of any country, it is necessary to seek the most remote and unsettled regions of swamp, moor, or mountain.

The origin of many cultivated plants, as we have seen, is very obscure, and it is evident that most of

the common domestic plants have been very much changed in the course of the centuries during which they have been cultivated. It is highly probable that the earliest agriculturalists took advantage of the variations which occur in wild plants, and that this process, in time, resulted in the widely different varieties which have replaced the primitive stocks, which in many cases we can no longer with certainty recognize. Hybridization has also undoubtedly played an important part in the origin of many cultivated races of plants, but it is not likely that this was consciously practised in early times, although it is not improbable that hybrids may have been responsible for some of the early cultivated plants.

**Plant Breeding.**—Of late years, however, the development of new forms of plants has been the deliberate aim of a host of experimenters, and hundreds or even thousands of well-marked varieties, often much more different in appearance from each other than are many natural species, have resulted from their labors. One has but to consider the enormous number of new varieties of almost any popular flower or fruit—apples, grapes, roses, narcissi, etc., which the catalogues advertise every year, to realize the part which man has deliberately played as a creator of new forms of plants. These may be the result of spontaneous variation and subsequent selection, or by skilful crossing of different species or varieties, the tendency to variation may be very

greatly increased, and a wider range of variation may be thus developed, of which the experimenter takes advantage. It is in this way that man has most conspicuously acted as a real creator of new plant forms, many of which, as we have said, are very different from any natural species. How far plants naturalized for a long time in a new country, either intentionally or otherwise through human agency, have become permanently altered, has been but little investigated; but it would certainly be very interesting to know whether or not weeds, for example, after two or three centuries, have diverged perceptibly from the type of the same species growing in the original habitat, and whether such differences would be lost if these plants were grown for a series of years in their old home.

**Changes in European Plants Introduced into America.**—It is well known that the standard fruits introduced into America from Europe have varied extremely, without any conscious selection on the part of man. This has been very carefully studied with reference to apples, especially, many varieties of which were introduced originally from Europe. By '1817, according to Professor Bailey, over 60 per cent of the best varieties in the United States were of American origin, and at present probably over 80 per cent are native varieties. Most of these American types do not succeed in England, owing to the different climatic conditions. It is quite probable that a similar study of the accidentally in-

roduced plants, like the weeds, would show much the same differences as a result of adaptation to the new climatic conditions, but it is not likely that these differences would be nearly so marked as in the cultivated species, which are notoriously variable.

While from very early times superior forms of fruits and flowers, which may have arisen by chance, were selected for cultivation, deliberate attempts to produce new forms by crossing, or special methods of cultivation and selection, seem to have been first practised towards the end of the 18th century. It is highly probable, however, that the Japanese and Chinese, who are such skilful horticulturists, practised this art long before scientific methods arose in Europe and America, but reliable information on this point is difficult to secure. The importance of selecting the best type of seed, in order to maintain an excellence in any strain, has been recognized from very early times, but that man is able to actually create new forms of life was not realized until quite recently.

**Early European Plant-Breeders.**—Among the earliest European horticulturists who worked along really scientific lines, there were two whose experiments were made during the latter part of the 18th century and the early part of the 19th century. These two men, Van Mons in Belgium and Knight in England, developed systems of plant-breeding which resulted in the production of many valuable

fruits, and had a great influence upon the methods of plant-breeding.

With the breaking down of the dogma of the fixity of species, especially due to Darwin's work, an impetus was given to experiments in originating new forms. Some of the results of these may be noted in the long list of new varieties of fruits, vegetables, and flowers, that appear in the florists' catalogues every year. Plant-breeding has now become a science, and the results of these experiments are often of quite as great importance scientifically, as they are commercially.

The history of cultivated plants in the United States is an interesting one. Most of the standard fruits, vegetables, and field crops were first brought from Europe to the Atlantic States; but in course of time the marked climatic differences between the United States and Western Europe began to change the characters of most of the cultivated plants, and new varieties appeared which departed so markedly from the parent stock that they were soon given special names. By the selection of the best of these native seedlings, most of the plant varieties now in cultivation have arisen. At present, at least in the Eastern States, comparatively few European varieties are grown, this being especially the case with the standard fruits—apples, pears, and peaches.

**Domestication of Wild Fruits.**—Still more important has been the domestication of the native fruits—grapes, crab-apples, gooseberries, raspber-

ries, plums, pecans, cranberries, etc. Some of the European fruits, as for instance grapes and gooseberries, do not thrive in the Eastern United States largely on account of diseases to which they are very susceptible. Our native vines and gooseberries, while much inferior to the European varieties, are practically immune to these diseases, and have through crossing and selection given rise to very much improved varieties, which yield a fairly satisfactory substitute for the more tender European sorts.

Much attention has been given of late years to the development of new varieties by crossing and selection. In this connection the work of Luther Burbank has for several years attracted much attention, and deservedly so, although his work has been very much over-exploited by newspapers and cheap magazines, in search of startling novelties. Burbank, through long years of experimentation, combined with an extraordinary natural gift for recognizing the essential characters of the plant with which he is working, has been able to accomplish what look like veritable miracles to the layman. However, most of his results have been obtained by the same methods of crossing and selection which all plant-breeders use. Some of his results are hard to understand, and offer some difficult problems to the student of heredity. Through the labors of Burbank, and other plant-breeders, many new and important varieties of cultivated plants

have been added to the long list of those previously grown.

**Recent Work in Introducing New Plants.**—Many new plants have been introduced from foreign countries—hardy wheat and apples from Russia, fitted to survive the severe climates of the Dakotas and Montana; dates from Northern Africa and Arabia have been planted successfully in the hot deserts of Arizona and Southern California; and very many other fruits and ornamental plants have come from various parts of the world. Especially is this the case with Japan, which has given to our gardens many of our choicest ornamental plants, and several valuable fruits. Japanese plants, as a rule, are particularly adapted to the Eastern United States, where they often do much better than European plants. The climate of Pacific Asia is very much like that of Atlantic North America, and Asiatic plants find themselves very much at home in the American gardens.

The great importance of the work of the United States Department of Agriculture, and the State Experiment Stations, in improving the character of agricultural and horticultural products of the country, need not be dwelt upon at length. By the study of methods of cultivation, and the improvement and selection of varieties adapted to different parts of the country, the study of plant diseases, and, last but not least, the introduction of new varieties from foreign countries, the wealth of the country has

been increased by a sum many times greater than the total amount spent in maintaining these experiment stations. As a result of this great work, by proper selection of varieties and improved methods of agriculture—e.g., dry farming in the arid West—the area of land fitted for agriculture has been very much extended within recent years, and land which for ages has remained a barren waste, now is compelled to yield its crops of grain and fruit as a reward for the ingenuity and persistence of man.

## CHAPTER X

### THE ORIGIN OF SPECIES

**T**HE mutability of all organisms is universally recognized by modern biologists, and the origin of new types or "species," as the result of such mutability, is no longer questioned. Many attempts have been made to explain the mechanics of the origin of species, and the laws governing them; but none of the very divergent theories proposed can be said to offer a satisfactory explanation of all the facts concerned.

**Experimental Morphology.**—For a number of years the efforts of many of the ablest biologists have been devoted to what has been called experimental morphology, or a study of the effects of various stimuli upon the structures of organisms. It becomes more and more evident that plants are astonishingly plastic, and respond very quickly to stimuli of many kinds which may exercise powerful formative effects upon their structures. Plants, being especially adaptable, and generally more easily handled than animals, have naturally received much attention at the hands of the experimenter, and the results of these studies have added much to our knowledge of the laws governing the development

of living things. The very readiness with which plants respond to stimuli is, however, a source of danger in making sweeping generalizations from insufficient data. Our ignorance of the internal mechanism of the cell, and the fact that often the full effect of a stimulus is not always immediately evident, make it necessary to exercise extreme caution in explaining the real significance of apparently quite obvious reactions to stimuli.

Another source of error is the too general application of results drawn from a study of plants to the behavior of animals under like conditions. While it is doubtless true that the protoplasm of plants and animals is, so far as we can judge, very similar in its composition, and in a general way reacts in much the same manner to similar stimuli, it must be remembered that the two kingdoms, plants and animals, have diverged further and further away from the ancestral organisms, and this divergence has resulted in sharply marked differences, both structural and physiological, so that we cannot safely argue from the behavior of one of the higher plants under certain conditions what would be the result upon an animal subjected to the same conditions. This can perhaps be best shown in considering the questions of reproduction and inheritance.

**Parallel Development of Reproduction in Plants and Animals.**—Plants and animals show a remarkable parallelism in the evolution of the reproductive

cells and the methods of fertilization, and this is also true of the evolution of the nuclei of the body cells. These resemblances are all the more wonderful, as it is difficult to see how one type could have been inherited directly from the other. At the time when plants and animals definitely parted company, sexuality was either not developed at all or was on a very low plane, and consisted in the simple fusion of two similar gametes or sometimes of two complete individuals. Moreover, the nuclei of these primitive organisms, such as the Flagellata, do not seem to possess the complexity of structure found in the nuclei of the higher plants and animals. Since the sexual elements of the higher plants and animals are independent developments, it is probable, in spite of the close resemblances, that there are inherent differences in their nature, corresponding to the differences existing in the bodies of plants and animals, and it is not likely that the laws governing the development of one will apply without exception to the other. We may, for instance, show that the early segregation of the sexual elements in many animals justifies the assumption of a special germ plasm; but if we try to apply this hypothesis to plants, it breaks down completely, as it is quite impossible to cite any evidence for such segregation of sexual cells in these organisms, which in very many cases do not arise from sexual cells at all and may be asexual throughout their whole existence.

**Imperfect Individualization in Plants.**—One of the greatest differences between the higher plants and animals is the imperfect individuality of the former compared with the more highly individualized animal. We have already pointed out that an oak is not an individual in the same sense that a dog is. Each leaf-bud of the tree is a potential individual, and the whole is a colony of like individuals, rather than a single organism. We may cut off a twig and plant it, and in time we shall have another tree with all its parts, including flowers, complete. There is here no question of the development of sexual cells from similar germs in the bud from which the tree grew, as there is absolutely no trace of any flowering structures, and it may be years before the new tree is large enough to produce flowers. Moreover, the tree itself is, properly speaking, asexual, sexuality being restricted to the insignificant gametophytes, arising respectively from the embryo-sac and the pollen-spore.

As the regeneration of the whole plant is possible from a mere fragment of a bud or leaf, the germ plasm, if it is present, must be distributed throughout the somatic tissues, and therefore exposed equally with them to the direct action of external stimuli. This lack of individuality and great power of regeneration, as well as the ready response to stimuli of various kinds, makes it hard to discriminate between what may be considered purely onto-

genetic or fluctuating variations, and those which may be assumed to be of hereditary value.

### VARIATION

That all organisms vary is plain from the most casual study. Not only are no two individuals exactly alike, but no two organs of an individual are identical. Thus it would be impossible to pick out two leaves or flowers which are the same in all respects. The source of these variations, and their value in the evolution of new species, are the questions which are engaging the attention of many biologists at the present time.

In attempting to determine the causes of these universal variations, we at once meet with an almost unsurmountable obstacle. It is practically impossible to determine to what degree the differences between two plants of the same species, growing under apparently the same conditions, are due to inherent peculiarities, and how much to extrinsic factors which may not be evident. That there are individual idiosyncrasies in plants, as well as in animals, is certain. No two individuals in a lot of seedlings will be exactly alike, and the differences may be very striking; but what causes the apparently greater inherent robustness, for example, of one and the weakness of another, is difficult to analyze. Whatever may have been the cause of the superiority of certain individuals, the superiority is evident, and must

give the plant a better chance in the struggle for existence. It does not necessarily follow that the more robust members of a lot of seedlings may be the ones that finally survive, as accidents may occur; they may be ravaged by insects or birds, and indeed might be preferred by these to their less vigorous competitors. But taking all things into account, it is reasonable to suppose that the more vigorous individuals will in the end get the advantage of their weaker rivals, and leave a larger number of offspring to transmit their more robust constitution.

**Continuous and Discontinuous Variation.**—Biologists recognize two main forms of variations, small or continuous variations forming a practically unbroken series, connecting the extremes within the species; and a second kind, the so-called discontinuous variation, where there is the sudden appearance of a character without intermediate ones between it and the type. Under the latter head are included the "sports" of the gardener, and the "mutations" of De Vries and his followers.

Fluctuating variations may perhaps best be studied in cultivated plants, especially those which are known to be true species, where variation is not due to hybridization. A single example will suffice to illustrate this point. I have recently had in my garden a large number of plants of *Cosmos*, a favorite autumn flower in California, and a good botanical species. The plants were of three varieties, white, pink, and crimson, and the variations

in other respects were very striking. In height the plants ranged from three to ten feet, and while these variations were due to some extent to the differences in the soil and moisture, the difference between individuals growing together was sufficiently striking. The flowers showed very great differences in size, in the form of the rays, and in the shade of color, ranging from pure white through various intermediate shades of pink and red to deep crimson. The leaves also varied greatly in size, breadth, and remoteness of their fine divisions. Similar variations might be cited for almost any cultivated species grown in quantity, and to a less degree for most wild ones.

The gardener by selection can easily control any of these variations, e.g., the color of the flower, and it is probable that natural selection could also take hold of such variations. If, for instance, crimson flowers should be more useful than white ones, it is quite conceivable that the white ones might be eliminated, as the result of natural selection alone.

**The Range of Fluctuating Variations Dependent upon the Nature of the Variation.**—The limits within which fluctuating variations may act undoubtedly depend very much on the character of the variation involved. There may, for instance, be physiological reasons which forbid variations in certain directions beyond a given point. Thus, for example, by selection the percentage of sugar in the roots of sugar beets has been doubled, but it has

been found almost impossible to increase the percentage materially beyond this point, presumably due to the fact that the constitution of the cells will not permit of higher concentration of the cell sap. It is probable that there are limits in size also beyond which certain forms cannot go. It is hardly likely that any amount of selection will enable the gardener to grow pansies as big as peonies, or cherries the size of oranges.

**Sports.**—Discontinuous variations have of late attracted much attention, owing to the important work of De Vries and his disciples. These discontinuous variations, or “sports,” have been long known and have given rise to many garden varieties of fruits and flowers. One of the best-known cases is that of the nectarine, which is a sport from the peach. The importance of De Vries’ work, which will be referred to presently somewhat more at length, is his systematic study of the origin of these sudden variations, and the demonstration that they may be made permanent, where crossing is prevented.

### ORTHOGENESIS

It is believed by many biologists that variation is often determinate, i.e., along definite lines, probably adaptive in their nature. If the definition of determinate variation, “Variation along special or particular lines of adaptation,” is accepted, there can be

no doubt that such determinate variation is a common phenomenon among plants. Among the most striking of these cases are the several quite unrelated cases of sex-evolution in the lower plants, as well as its development in animals, and also the remarkable resemblances already referred to in the structure of the nuclei and the complex details of nuclear divisions in plants and animals. The striking similarities in the evolution of the flowers in monocotyledons and dicotyledons are also an excellent example of such determinate variation. The development of sympetalous flowers has occurred a number of times in both monocotyledons and dicotyledons, and the same is true of the inferior ovary, and the development of zygomorphic flowers, which characterize the most specialized types in both classes. These have been developed quite independently in response to the same needs, in this case pollination by insects and birds. The development of special colors in flowers as a means of attracting birds and insects, e.g., the frequent occurrence of bright scarlet in ornithophilous flowers, and the development of nectar and scent, may very well be cited as examples of such definite or determinate variation. Many other instances might be cited, but one more will suffice. The character of the leaves of whole families or genera is often as characteristic as the flower. In the vetches we expect to find the tendril always assuming the place of the terminal leaflet, while in *Smilax* quite as uniformly

we find it developed from the base of the petiole. The replacing of the primitive leaf by vertical phyllodes in many species of *Acacia* may be also considered as a case of determinate variation, and the many more that might be cited all tend to show that the essential organization of all the higher plants, at least, is sufficiently alike to produce much the same reactions in response to similar stimuli, so that there is a marked similarity in the structures resulting from adaptation to special conditions in various lines of development.

**Variation Greatest in Lately Developed Characters.**—In his studies on variation, Darwin emphasizes the fact that variability is much more marked in what one may assume to be later developed characters. Thus generic characters are less variable than specific ones, and wild species are very much less variable than cultivated ones. Just what constitutes a "species" is more or less a matter of personal opinion. How far such varieties as those described by De Vries, which can be maintained by artificial selection, can be called species, is not an easy matter to decide. Many cultivated races of both plants and animals, which are undoubtedly variations from some single recognized species, differ far more widely from this and from each other, than is the case among many wild species, or sometimes even genera; but the purity of such artificial species can be maintained only by careful artificial selection. Even in nature the

limits of species are often very difficult to decide, and no two students of any large genus of plants agree exactly as to the number of species within the genus. How these species have originated is a vexed question which for the last generation has aroused an amount of speculation, and even acrimonious controversy, that would seem to show that men of science are not much behind the theologians in their defense of the true faith against the attacks of heretics.

### THEORIES OF EVOLUTION

The idea of evolution is a very ancient one, but until the 19th century evolutionary theories were too vague to attract any general attention. Darwin's great service to science is not that he first enunciated the principles of evolution, but that by rigorous experiment and observation he made the fundamentals of evolution so clear that henceforth they could not be ignored. Especially did he make evident the enormous importance of natural selection in the evolution of new forms of life, and the origin of species. As Darwin's studies included plants as well as animals, and covered an extensive range of topics connected with some of the most important botanical problems, the debt of the botanist to Darwin is a very great one. The botanical student will remember, however, that during the ten years preceding the appearance of Darwin's

"Origin of Species," the German botanist, Hofmeister, published a series of researches upon the comparative morphology and development of the higher plants, that were truly epoch making; for while he did not expressly enunciate the theory of evolution, his whole work was based upon the assumption that the seed-plants were derived from the ferns, which in turn were the descendants of moss-like progenitors. While most of his work has been amplified and corrected in the light of new discoveries and by the aid of improved methods of research, nevertheless the fundamental principles of his work remain to-day as the basis of the comparative morphology of the higher plants.

**Neo-Darwinism.**—As is so often the case, the disciples have gone far ahead of their master in upholding his theories, which have assumed for them the form of a veritable dogma. Some of the followers of Darwin have assumed the omnipotence of natural selection, in which they see the only factor in evolution, denying that environment can have any direct effect in modifying an organism, or at any rate that any such change can be transmitted to its offspring. As every reader of Darwin knows, he fully recognized the importance of environment as a formative agency, and was perfectly aware of the value of much of the work of Lamarck, his great predecessor, who was not appreciated during his lifetime, but who has been valiantly defended by a host of ardent advocates during the

past generation. These Neo-Lamarckians have arrayed themselves against the Neo-Darwinians, who claim that they, and they alone, are truly orthodox. Much ingenuity has been expended in the elaboration of theories which shall prove one side or the other, but it must be confessed that to the outsider these theories often savor more of metaphysics than of natural science. For an admirable summary of the present status of evolutionary theories the reader may consult Professor Kellogg's recent work, "Darwinism To-day."

Let us briefly examine the testimony of plants as to the method by which new forms arise, or if you will, the methods of the origin of species.

**Natural Selection.**—The essence of the Darwinian theory is that species have arisen by natural selection, as the result of the struggle for existence necessitated by the fact that there are always many more individuals produced than can possibly come to maturity. Darwin believed that natural selection acted upon the slight fluctuating variations which constantly occur in all species, but he also recognized the possibility of new species being started by discontinuous variations, or sports, although he considered these of secondary importance in species forming. That natural selection does act is easily enough demonstrated by direct observation; but it is not so easy to show *why* certain individuals survive while others perish. While in a general way it may be assumed that the fittest survive, this does

not by any means necessarily follow, as accidents may result in the destruction of the most vigorous forms while the weaker survive to multiply their kind. Thus in a lot of seedlings exposed to the attacks of insects, birds, and other enemies, there seems to be little discrimination, and the vigorous young plants are perhaps even more likely to suffer than the weaklings. Darwin assumes that there may be developed as the result of natural selection protective devices, as, for example, poisonous or offensive secretions, which may render the plants distasteful, and of course it is the individuals in which these characters are most pronounced which will be most likely to survive. Unfortunately the demonstration of this hypothesis is by no means easy.

There is no question about the variability of all species. Not only does the same plant vary under different conditions, but among young seedlings growing under apparently exactly similar conditions a large amount of variation can be observed, and one must admit that the variation in many cases must be considered as the result of individual peculiarities, not to be explained as the result of any evident environmental factors. Within the limits of any species there may be a decided range of variation, often showing a wide departure from what may be called the mode or type. Such slight differences are especially common in certain genera, and are the source of endless confusion in attempting to define the limits of species. In Europe the

genera *Hieracium* and *Rubus* have been split up into very many species by some botanists, while others reduce them to a small fraction of these, regarding the differences as not sufficiently definite or constant to warrant raising these varying forms to specific rank.

In America, at the present time, there is a strong tendency to treat some of our native genera in much the same manner. The Thorns (*Cratægus*) offer a notorious example of this. In the latest edition of "Gray's Manual" sixty-five species are described, while in the edition of 1868 but nine species were recognized. Unfortunately it is impossible to trace the pedigree of any of these forms, and whether they have arisen by the accumulation of small differences, or whether they are the results of discontinuous variations or mutations, we are not in a position to say.

**Artificial Selection.**—Perhaps the strongest evidence offered by plants for the truth of the Darwinian theory of natural selection, is the origin of new forms under cultivation by selection alone. In this way, for instance, the amount of sugar in the root of the sugar beet has been doubled, and the percentage of quinine in the bark of certain varieties of *Cinchona* has been very largely augmented. Many varieties of flowers and vegetables have also resulted from pure selection. Among Burbank's many interesting results is one which illustrates the origin of a new form by selection alone. From

the vivid orange-yellow California poppy he has developed a bright red variety by selecting individuals which showed traces of red in the petals, and then by successive selection of the offspring, the red color was intensified until a pure red flower resulted. Similar examples of such selections can be shown in the development of many cultivated plants, and thus it is proved that under certain conditions, at least, selection alone is sufficient for the origin of new forms. Whether or not natural selection is the usual form of the *origin* of new species, there can be little doubt that it is an essential factor in maintaining the new form after it has once appeared.

#### LAMARCKISM

**Modifications in Cultivated Plants Due to Changed Environment.**—No student of plant-behavior can doubt that the structure of the plant is readily affected by its environment. Changes in the environment are quickly reflected by changes in the structure of the plant. As we have already considered this at some length in a former chapter, the matter will not be enlarged upon here. The question naturally arises: Are the ontogenetic changes due to environment capable of transmission? To this the experimenter answers at once, They certainly are. Striking instances of this are the numerous cases of acclimatization. Races of domestic plants, e.g.,

corn, from the Southern States, where the growing season is long, require a much longer time to come to maturity, and the seed of such races planted at the North will often fail to mature the first season, but if any of the seed is matured and planted a second season, the time of maturity will be markedly less, and this peculiarity is transmitted so that in the course of a few generations a race is developed which is fitted to the shorter seasons of the North. It has been observed that in the United States the European varieties of apples, pears, and some other fruits have given place largely to new forms which have arisen often spontaneously, as the result of new climatic conditions in America. Moreover, the eastern varieties of fruits grown in the Northwest and on the Pacific coast, have become similarly changed, apparently in response to different climatic conditions, and these changes are heritable.

It is now a common practice to grow seeds of many vegetables and flowers for the eastern trade, under the very favorable climate of the coast valleys of California, where the long dry summers permit very perfect maturing of the seed. It has been found, however, that from time to time, seeds grown in the East must be sent back, otherwise there is a tendency to produce a plant which will require for its growth a longer time than is furnished by the short eastern summer. Many plants in the California gardens also require a much longer period of growth

before they flower, this being notably the case with many bulbous plants.

**Experiments with Alpines.**—Some very interesting experiments have been made by Bonnier and other students upon alpine plants, which illustrate very clearly the hereditary character of changes induced by altered environment. In some cases a plant was divided into two portions, one being grown at a low altitude, and the other transferred to an alpine station, where it was grown for several years. The latter in time developed the dwarf habit, and several other characteristics of a true alpine plant. After several years, these artificial alpine plants were returned to the old environment, and it was found that they gradually reverted to their original form, and that the time necessary for this was approximately the same as that required to make the change to the alpine type. It is a fair assumption that a plant transferred to a new environment, and subjected to this for a long period, would to all intents and purposes thus become a new species, and it is not likely that, if after a thousand years it were returned to its old environment, it would ever revert exactly to its original condition.

It is probable that a critical study of plants long naturalized in a new country would show marks of constant change from the original type. It would be interesting to know, for example, whether the common European weeds that have been naturalized in the United States for two or three hundred years,

have in that time changed sufficiently to make them greatly different from their European prototypes. If such changes have taken place, it would also be interesting to know whether taken back to the old home they would revert perfectly to the original type. A critical study of this kind might very well throw much light upon the mechanics of species making. Bumpus made a study of the English sparrow in the United States, and he found that a perceptible modification had arisen in the bird since it was introduced into the United States, some thirty years earlier. Considering the readiness with which plants vary, and the very much longer time that many weeds have been naturalized in America, it would be expected that a certain amount of change had taken place.

The conclusion to be drawn from a study of the behavior of plants seems to be that both fluctuating and discontinuous variations are important in species forming. The effect of environment upon organisms is unmistakable, and these effects are, sometimes at least, transmissible to a greater or less extent. This variation offers the handle for natural selection to grasp, and the permanency of any variation must depend upon natural selection.

### THE MUTATION THEORY

The most notable theory of evolution that has appeared of late, is the Mutation Theory of De Vries.

His book, "Die Mutationstheorie," published in 1901, attracted at once much attention, and was a great stimulus to the further study of variation in both plants and animals. The basis of this theory is that new species arise, not by the accumulation of slight or fluctuating variations, but by discontinuous variations or sudden leaps, which are immediately of specific value.

**Discontinuous Variations: Sports.**—Reference has already been made to these discontinuous variations, or sports, of which many have been recorded, especially in cultivated plants. A list of the most important of these has recently been given by Lotsy in his work, "Vorlesungen über Descendenztheorien," 1906. The first of these recorded mutations dates back to 1590, when there appeared in the garden of the Apothecary Sprenger, in Heidelberg, a well-marked variety of *Chelidonium majus*, which proved to be constant and reproduced itself perfectly from seed, thus behaving like the "mutants" of De Vries. A very widely cultivated plant which is supposed to be a mutant, is the well-known Lombardy poplar, which has been propagated in a purely non-sexual way for a very long time. It is supposed to be a sport from the European *Populus nigra*. All of the individuals that are known are staminate, and consequently cannot propagate from seed. The purple-leaved, and cut-leaved, varieties of many trees and shrubs, are probably examples of such sports, and many at least have been found to

reproduce themselves from seed if care is taken to prevent crossing. A recently described example of what appears to be the appearance of a new species by mutation, is that of *Capsella Heegeri*, described by Solms-Laubach, who considers it to be a new species derived by mutation from the common shepherd's-purse, *C. bursa-pastoris*.

**De Vries' Studies on the Evening Primrose.**—The theory of De Vries is based principally upon a very extensive series of studies of the variation in an American plant, the large flowered evening primrose, *Oenothera Lamarckiana*. This plant was found growing wild near Amsterdam, where it had evidently escaped from cultivation, and an examination showed that it was in a very variable condition. For a series of years the plant was kept under observation, and many cultures were made, with the result that certain marked variations were found to appear repeatedly, and these varieties, or incipient species, according to De Vries, were nearly always constant, when kept from crossing with other varieties, or with the original type. From the behavior of these "mutants," as De Vries called these varieties, he came to the conclusion that new species always arise by such discontinuous variations, and their persistence as permanent species depends upon whether or not they survive as the result of natural selection.

**De Vries' Theory of Pangenesis.**—De Vries believes that heredity is to be explained by the assump-

tion that the sexual cells contain certain structures, "pangenes," which are the transmitters of hereditary characters. He assumes also that there are certain periods in the history of the species, when for some reason a state of great instability and great variability prevails, and that at such periods mutations occur. A mutation is to be explained by the development of an additional one of the "heredity bearers" in the germ cells of the mutant, or by the destruction of one of these; while in mere varieties, the number of these hereditary units is the same as in the parent species, but one or more of them may remain latent. While such an explanation is logical enough, it must be confessed that it is quite incapable of proof, and may very well be regarded with some skepticism.

De Vries' experiments on *Oenothera Lamarckiana* have been repeated in America, especially under the direction of MacDougal in New York, and the results are entirely in accord with those obtained by De Vries.

Darwin regards the accumulation of slight fluctuating variations as the basis upon which natural selection works, while De Vries contends that these fluctuating variations are of no value in evolution, and that mutations alone are important; but he agrees with Darwin that the variation, once established, must depend upon natural selection for its maintenance. Whether the mutation theory will prove the all-sufficient explanation of the origin of

species is extremely doubtful, but the clear demonstration of the nature of these discontinuous variations, and the fact that they do offer a rational explanation for the origin of species, makes the work of De Vries of very great value.

**Criticism of De Vries' Work.**—The most serious criticism of De Vries' work is the uncertainty of the origin of the species upon which he worked. *Oenothera Lamarckiana* is not known at present in a wild condition, and Bateson has gone so far as to suggest that it is itself a hybrid, and recent experiments by Davis indicate a possible origin of *O. Lamarckiana* from a cross of *O. biennis* and *O. grandiflora*. If such should be the case, Bateson further says that the alleged mutants may be only reversions, or "recessives," in the Mendelian phraseology. The occurrence of other similar mutants, which are certainly not of hybrid origin, however, and which are capable of breeding true, would indicate that the mutants of De Vries are not merely recessive hybrids.

Lotsy, in the work already referred to, suggests a very probable cause for the origin of mutants which does not involve the idea of special "inheritance units." His view is that the tendency to mutation does not lie in the egg-cell, or sperm, but arises subsequent to fertilization as the result of the mating of the most dissimilar gametes, which would naturally only occur rarely.

## HEREDITY

**Chromosomes the Bearers of Heredity.**—The mystery of heredity has always aroused the interest of biologists, and many ingenious theories have been propounded to explain it, but all of these are more or less unsatisfactory, as they assume premises which are impossible of demonstration. The facts of fertilization, as they have been studied in both plants and animals, indicate that the sexual nuclei are undoubtedly the most important parts of the cell in the sexual process, and Strasburger believes that in the higher plants the chromosomes alone are potent as the bearers of heredity, since only the sexual generative nucleus from the pollen-tube enters the egg-cell. We must remember, however, that in the lower plants the whole protoplasts of the gametes fuse, cytoplasm as well as nuclei. Moreover, it must not be forgotten that in very many plants inheritance is through nonsexual methods, principally by budding, where there is no development of special reproductive cells as is the case in sexual reproduction.

If the chromosomes are allowed to be the vehicles of transmission of hereditary characters, it still remains to be explained how this is accomplished. The assumption that they contain innumerable "determinants" which correspond to the special structures of the adult, is a simple explanation, but not a satisfactory one. De Vries' theory of "pan-

genes" is more likely to approximate the truth. These ultimate structural units of the cell are supposed to be of relatively few kinds, but capable of an infinite variety of combinations. De Vries compares them to the letters of the alphabet, which are capable of combination into an almost infinite number of words. It may be questioned, however, whether specific differences necessarily involve new kinds of pangenes, as De Vries believes to be the case.

**Heredity a Physiological as well as a Morphological Question.**—The investigations of experimental morphology are making it more and more likely that the effects of extrinsic stimuli are potent in heredity, and that heredity is quite as much a physiological problem as a morphological one. This view has been set forth in a particularly striking fashion by Professor F. Darwin, in his recent address as president of the British Association for the Advancement of Science. Professor Darwin argues that the effects of stimulation may be cumulative, and transmissible, and that the ordered sequence in the development of the individual, "the rhythm of ontogeny," is, as he puts it, a habit. It has been shown by many experiments, e.g., those of Jennings on the infusoria, that the effect of repeated stimulation is a different reaction on the part of the cell to the later stimulus. The "physiological state," to use Jennings' phrase, is altered, and a habit is established.

F. Darwin borrows from Seman the word "engram" to indicate the effects of a stimulus upon the protoplasm, and Darwin argues that these engrams are permanent and transmissible from cell to cell. As he explains it the engrams, or results of stimulation, are of the nature of memory. "My view is that the rhythm of ontogeny is actually and literally a habit. It undoubtedly has the feature which I have described as preëminently characteristic of habit, viz., an automatic quality which is seen in the performance of a series of actions in the absence of the complete series of stimuli to which they (the stages of ontogeny) were originally due. This is the chief point on which I wish to insist: It means that the resemblance between ontogeny and habit is not merely superficial, but deeply seated. . . . It cannot be denied that the ontogenetic rhythm has the two qualities observable in habit—namely, a certain degree of fixity or automaticity, and also a certain variability. It is not irrevocably fixed, but may be altered in various ways. Parts of it may be forgotten or new links may be added to it. In ontogeny the fixity is especially observable in the earlier, the variability in the later, stages."

Darwin's mnemonic theory does not involve the assumption of special determinants or pangenesis, and as we have already pointed out in Chapter II, the similarity in the constitution of the egg, and the subjection of the developing embryo to practically iden-

tical conditions, are sufficient to account for the principal phenomenon of hereditary transmission without the assumption of the presence of a special germ plasm. This view frankly admits that the development of the organism not only may be directly influenced by external factors, but that the changes so induced may be inherited.

**Mendel's Law of Heredity.**—Some 40 years ago a German monk, Gregor Mendel, published in the proceedings of an obscure scientific society the results of a series of experiments upon the laws of heredity. These were quite ignored by the scientific world until attention was called to them by De Vries and some other experimenters, almost simultaneously, in connection with the revived interest in the study of heredity, aroused by De Vries' work on mutation. The great value of Mendel's work lies in its showing that there are definite laws governing the inheritance of certain characters. Mendel worked especially upon varieties of garden peas, and demonstrated that where any two contrasting characters were crossed, as for instance long stems and short stems, smooth and wrinkled seeds, that these characters were inherited in definite proportions, and one of the characters was "dominant" while the other was "recessive." For instance, when a variety with round seeds is crossed with one producing wrinkled ones, when these are self-fertilized, the progeny will all produce seeds of the round type, which is thus shown to be dominant.

The plants resulting from the round seeds of the second generation, however, are not all alike, but some will produce round seeds while others show the wrinkled seeds, and the proportion in which these are produced will be three plants with round seeds to one plant with the wrinkled seeds. The offspring of the latter, or recessive type, will breed true, but of the three-quarters with the round seeds only one-quarter are pure dominants, breeding true, while the offspring of the other half are hybrids, dividing in the next generation in the same ratio, three dominants to one recessive, and so on. This behavior implies that the sex cells are either pure dominants or pure recessives, and when fusing in crossing will produce either pure dominants, recessives, or hybrids between the two, the proportion following closely the law of probability.

Professor Bailey explains the law as follows: "Differentiating characters in plants reappear in their purity and in mathematical regularity in the second and succeeding hybrid offspring of these plants; the mathematical law is that each character separates in each of these generations in one-quarter of the progeny and thereafter remains true. In concise figures it is expressed as follows:  $1D : 2DR : 1D$ .  $1D$  and  $1R$  continuing true, but  $DR$  breaks up again into the dominants and recessives in the ratio of three to one."

The Mendelian law has been applied to a good many cases of inheritance in both plants and ani-

mals, and has proved true in many instances, although there are numerous exceptions for which as yet there is not an adequate explanation.

### THE EVOLUTION OF SEX

The characters of the sexual cells in plants and animals often show extraordinary similarity, and the details of fertilization are very much the same. On account of these similarities it is commonly assumed that the nature of sexuality in plants and animals is identical, but a careful examination of the phenomena connected with the sexual process in plants and animals will show differences which are sufficiently striking to make one cautious in drawing too comprehensive conclusions as to the nature of sexual reproduction in general.

**Evolution of Sex in Plants and Animals Not Identical.**—Although the nature of the sexual cells in the higher plants and animals is apparently so much alike, the history of the evolution of sex in plants and animals has been apparently quite different. In animals, sex is far more important than in plants, and seems to have been established once for all. All Metazoa are sexual at some stage of their development, and there is no existing evidence of that transition from the non-sexual condition to the sexual which is shown so clearly in several evolutionary lines in the plant kingdom. Between conjugation of two individuals found in the Infusoria,

and the clearly differentiated eggs and sperms of the lower Metazoa there are no intermediate stages. With the increasing individuality shown by the higher animal types, the sexual elements become more and more sharply segregated from the somatic tissues, and the direct derivation of the generative tissues of one generation from those of the preceding one looks very plausible, and the theory of a definite germ plasm handed on from one generation to another has a basis of actual observation.

**Sex has Arisen Repeatedly in Plants.**—Sex in plants has evidently arisen over and over again. In some half a dozen quite unrelated groups among living plants, every stage of development of the gametes can still be found, from nearly or quite similar isogametes, to perfectly differentiated eggs and sperms. It is also clear that the simpler types of gametes are derived from non-sexual zoöspores, or from non-sexual individuals in the case of unicellular plants. The slight difference between the sexual and non-sexual cells is shown by the ease with which some of the lower plants may be forced to produce one or the other as the result of different stimuli. Klebs' experiments upon various algæ and fungi are especially striking as showing how readily the character of the reproductive cells may be controlled.

While the mechanism of fertilization may be very much the same in plants and animals, the results are usually very different. The fusion of the egg-

cell and sperm is effected much in the same way, but the history of the zygote in animals and plants is, as a rule, not at all alike. In the animals the egg develops at once into the embryo, which sooner or later, either directly or after a metamorphosis, becomes a single individual like the parent. This is rarely the case in plants. In the green algæ, the zygote usually becomes a resting spore, whose main function is to carry the plant over periods of stress. Only rarely, and this is especially the case in such marine types as *Fucus*, does the zygote develop at once into the definite plant. In the majority of the fresh-water algæ, as we have seen, the development proceeds only after a period of rest, and though the zygote may germinate directly into a new plant, much more commonly it first divides into a number of free cells, each of which gives rise to a new individual, and this interpolation of a neutral stage between the zygote and the production of new sexual plants, becomes more pronounced in the higher plants.

While the alternation of generations, which is so conspicuous in all green plants above the algæ, is sometimes met with in animals, as in some insects and hydroids, it is far less common than in plants. In all of the higher plants, from the ferns to the seed-plants, it must be remembered that the predominant phase is the non-sexual sporophyte. Much confusion has arisen from overlooking this fact. The sexual cells of a flowering

plant are not parts of the sporophyte at all, but belong to the insignificant sexual generation, or gametophyte, included within the ovule, or developed from the pollen-spore during its germination. The embryo develops, not into a gametophyte like the plant which produces the egg, but into a sporophyte, which produces non-sexually myriads of spores, embryo-sacs or pollen-spores, which in turn develop the gametophytes. A single fertilization, therefore, results ultimately in an enormous number of new gametophytes, although years may elapse before the sporophyte becomes large enough to flower and produce its crop of spores. Now to assume that there is a special germ-plasm, which is passed on from the tiny gametophyte to the non-sexual and long-lived sporophyte, and finally segregated in the spores, and again passed along to the next generation of gametophytes is, to say the least, improbable.

#### **Subordination of Sex in the Higher Plants.—**

The relative unimportance of sex in plants is shown by the predominance of the asexual condition in all of the higher plants. It is in the more primitive aquatic forms, like the algæ or the amphibious archegoniates, that sexuality is best developed, and it is evident that this is directly associated with their aquatic life, as in these plants the sperms are motile and require water for their transport. In the more highly developed land plants sexuality becomes more and more subordinated, and not in-

frequently may be entirely suppressed, the sporophyte multiplying itself solely by vegetative division. Some seaweeds and many fungi appear to be also entirely sexless, and it is hard to see wherein these plants are inferior in size or structure to the sexual types. This subordination of the sexual conditions in so many plants is in striking contrast with the universal occurrence of sexuality in the Metazoa. It may be safely asserted that the substitution of asexual reproduction for the sexual method in plants is largely due to the generalized character of their tissues, the cells being far more plastic than those of the more highly specialized animals, and therefore capable of an almost unlimited degree of regeneration.

### THE SIGNIFICANCE OF SEX

The underlying reasons for the development of sex have been the subject of endless speculation, but there is no general agreement among biologists as to what these causes are. Most of these speculations have been from the zoölogical side, and it is at least doubtful whether they will apply equally to plants, where sexual differentiation might very well have arisen in response to quite different causes. In animals it has been assumed that there is a "physiological need" for fertilization, but just what this is, is not explained. Fertilization, or the union of two gametes, has been considered advantageous both

as an inducement for variation, and for the preservation of hereditary characters; but even among animals, as Kellogg has shown from his studies on both bees and aphides, the individuals produced by parthenogenesis are quite as variable as those developed from fertilized ova.

In following the history of the lower plants, it is very evident that the result of fertilization, whatever may have inaugurated it, is twofold: first, the development of a resting stage for carrying the plant over unfavorable conditions of drought or cold; and second the increased production of new plants, as each zygote usually produces more than one plant on germination. The second cause is probably the more important factor in the evolution of sex in plants, and it has been closely associated with the production of the resting stage, or terrestrial phase, in the green algæ and their descendants, the archeogonites; but in the strictly aquatic seaweeds, the rapid multiplication by zoöspores is quite sufficient, as no resting stage is necessary, and where an elaborate sexual system is present, as in the red algæ, the same object is attained by the development of a sporophyte from which numerous spores are produced without any resting stage.

The better development of the sexual cells in the fresh-water green algæ when compared with their marine relations, as well as the usual low grade of sexuality, or its complete absence, in the brown algæ, and certain green seaweeds, implies that there is

some connection between the conditions of life in fresh water and the evolution of sexual cells. This may, perhaps, be sought in the necessity for most fresh-water plants to provide resting stages. The zygote resulting from the union of two small, similar gametes is provided with a smaller amount of food material than is the case where there are well-developed sexual cells, large eggs and small sperms. Moreover, the larger amount of contents in such a large spore allows for a greater number of spores on germination, and so might be an advantage. Whether the fusion of the gametes provides a greater store of energy as well, can hardly be proven, but it is not at all unlikely. It is thus quite conceivable that the need for a resting stage fitted to produce quickly a number of germs at the end of the dormant period, was the most important factor in the specialization of the sexual cells in the fresh-water algæ. The further evolution of the zygote, as shown in the highly complex sporophyte of the terrestrial plants, has been sufficiently dwelt upon in an earlier chapter. The absence of any need for the terrestrial resting stage in the green and brown seaweeds may, perhaps, explain the generally low type of sexual cells in these forms.

The peculiar type of reproduction in the red algæ has evidently arisen quite independently, and the peculiar spore fruit has its nearest analogy in that of certain fungi. It will be noted that in the red algæ also, the fertilized cell does not produce new

plants like the parent, but a sporophyte bearing many asexual spores, so that, as in the green algæ, a single fertilization results in the production of many new individuals.

#### HYBRIDIZATION

**Natural Hybrids.**—It was long the general belief that true hybrids were necessarily sterile, but experiment has shown that hybrids may be quite as fertile as the parent species, or even in some cases may surpass them in fertility. This at once opens up the question whether new species may not sometimes arise immediately as the result of crossing of two other species, and there is abundant evidence that this is sometimes the case. While hybrids are usually of rare occurrence in nature, there are many records of such, and in some cases they occur in numbers equal to the parent species, and are apparently quite as well fitted to survive. These natural hybrids have been much more carefully studied in Europe than in America, where the number of authentic cases is relatively small. Kerner estimates that about one thousand natural hybrids have been found in Europe, but of these only a small number have survived and perpetuated themselves. As these latter may be perfectly fertile and apparently fitted to their environment, it is hard to see why they should not be considered as good species. Most of these were described as valid species before their

hybrid nature was recognized, and some of them have been repeatedly produced by artificial crossing of the parent species. *Narcissus poeticus* crossed with the daffodil (*N. pseudo narcissus*) produces *N. incomparabilis*, a favorite garden form which, however, has also been found repeatedly occurring wild where the two parent species grow near each other. *N. odoratus* has also been shown to be a cross between *N. poeticus* and *N. jonquilla*. A species of Foxglove, *Digitalis purpurascens*, is a cross between *D. purpurea* and *D. lutea*, and the hybrid alpine rose, *Rhododendron intermedium*, of the Tyrol, grows with its parents, *R. ferrugineum* and *R. hirsutum*, being sometimes more abundant than either of the parent forms.

One of the most remarkable of the hybrids is an orchid, *Nigritella suaveolens*, which often occurs in large numbers in the alpine meadows, and has been shown to be a cross between *N. angustifolia* and *Gymnadenia conopsea*, belonging to a different genus. The orchids, however, are often more fertile with pollen from other species or even other genera, and many bi-generic hybrids are known to the florist. It is even possible for plants belonging to different families to cross. A hybrid has been described (see Vernon, "Variations of Plants and Animals," page 166) between *Digitalis ambigua* (*Scrophulariaceæ*) and *Sinningia speciosa* (*Gesneraceæ*).

In the United States a number of hybrids have

been described among the willows, oaks, and sedges, and probably many more remain to be recorded. Of the oak hybrids may be mentioned that between the white oak and the bur oak, and a species described as *Quercus brittoni* which was shown to be a cross between *Q. Marylandica* and *Q. ilicifolia*. A fern, *Asplenium ebenoides*, is supposed to be a hybrid between the walking fern (*Camptosorus rhizophyllus*) and *Asplenium ebeneum*.

**Artificial Hybrids.**—The first artificial plant hybrids of which there is a definite record was obtained in 1760 by Kölreuter, whose further work in hybridization was very important, although not fully appreciated by his contemporaries. His first hybrid was obtained by crossing two species of tobacco, *Nicotiana rustica* and *N. paniculata*. Later he made experiments with many other genera, and demonstrated most of the important phenomena connected with the crossing of plants. Subsequently a long controversy arose over the question of the sterility of hybrids compared with species, which lasted for a long time. It is now clear that while as a rule sterility results from crossing widely different forms, e.g., different genera, this is not necessarily the case, and fertility or sterility of the offspring cannot be taken as the test for the validity of a species. The importance of hybridization in causing plants to vary has been taken advantage of by the plant-breeder, some of whom, like Burbank, rely frequently upon such crossing, not only to unite cer-

tain desired qualities, but also to disturb the equilibrium of the species and induce wider variation, which may thus be taken as the basis for selection.

**Aberrant Hybrids.**—Hybrids between two distinct species are usually intermediate in character between the parents, but this is not always the case. Sometimes one or the other parent is prepotent, or certain parts may be inherited from one and some from the other. Thus the flower of the hybrid may resemble one parent, and the leaves the other. Sometimes, however, the results of hybridization are most unexpected, and the hybrid differs markedly from both parents. This is the case in the *Primus* blackberry, produced by Burbank from the crossing of a wild California species, *Rubus ursinus* and *R. crataegifolius* from Siberia. The hybrid differs strikingly from either parent, and comes true from seed, and might very well be described as an entirely new species. Burbank has obtained similar results in hybrid walnuts, produced by crossing the native California walnut with the English walnut and the black walnut of the Eastern States. In every case the hybrid was distinguished by its extraordinary vigor, growing with wonderful rapidity, and far surpassing either of the parents in this respect. Moreover, in many cases the nuts produced by the hybrid were much larger than those of either parent. A cross made by Burbank between a yellow and a white poppy resulted in a flame-colored flower,

quite unlike either of the parents. The latter hybrid Burbank considers to be a case of reversion, but this, however, may be questioned.

Thus we see that as the result of crossing between markedly different forms, quite new types of flowers and fruits have been developed. Many artificial hybrids of orchids have resulted from crossing widely separate species, or even genera, and many of the novelties offered from time to time by the florists are hybrids, sometimes combining characters derived from several species. An example of one of these compound hybrids is the Shasta daisy, which is one of Burbank's "creations." The "Plum-cot" is a cross between the plum and apricot, and the Loganberry, now one of the standard fruits of California, resulted from crossing a native blackberry with the red raspberry. Among the most interesting of the recent hybrid fruits are Webber's Citrus-hybrids. Among these is the "Citrange," a hybrid between the hardy Japanese *Citrus trifoliata* and the sweet orange, which it is hoped may prove the beginning of a race of hardy sweet oranges. Another interesting hybrid is the "Tangelo," a cross between the grape-fruit or pomelo, and the Tangerine orange.

The plant-breeder takes advantage of the instability produced by changed environment, but since the time of Kölreuter's early experiments in hybridization, the great importance of crossing different forms to induce variability has been clearly recog-

nized. Kölreuter emphasized the importance of crossing, and also enunciated the principle that variability was very much increased by crossing hybrids, either with each other, or with the parent form.

**Graft Hybrids.**—There has been much controversy as to the possibility of hybrids arising from grafting. Several cultivated forms are alleged to have so arisen, but further attempts to reproduce them in this manner have been unsuccessful, and the question is still open whether the best-known cases of such alleged graft hybrids, the *Cytisus adami* and the *Cratægomespilus*, are not really hybrids of the usual type.

That hybrid grafts are possible has recently been shown by Winkler ("Berichte der Deutschen Botanischen Gesellschaft," 1907), who succeeded in producing an unmistakable hybrid by grafting a nightshade, *Solanum nigrum*, upon a tomato. After the nightshade graft had united with the stock, the latter was cut off so as to expose a flat surface, which included the united tissues of the scion and stock. From this cut surface there arose numerous adventitious buds, one of which developed into a shoot which was a compound of the tomato and nightshade. It was a "mosaic," one half being tomato, the other half nightshade, and some of the leaves were intermediate. Winkler proposed the name "*Chimæra*" for such vegetable monsters as this. Later experiments resulted in the production

of true graft hybrids, which were almost exactly intermediate in all respects between the nightshade and tomato.

### EXPERIMENTAL MORPHOLOGY

Much attention has been given of late to the experimental study of the formative effects of environment upon the developing organism. Both zoölogists and botanists have become much interested in this question, and many important works have appeared during the past few years. While caution is necessary in deducing from the results of these artificial experiments, the laws governing the development of organisms under normal conditions, nevertheless much light has been thrown, by these experiments, upon some of the fundamental problems of evolution.

One fact stands out especially prominent, namely the remarkable plasticity of the plant-organism, which responds readily to a very great variety of stimuli and shows an extraordinary range of variation within the species. These experimental studies also demonstrate very forcibly the generalized character of the plant tissues, and the readiness with which one organ may take over the functions of another when it is necessary. Space forbids more than a very brief reference to a few typical instances.

The leaves of many plants, e.g., roses, peas, are

provided with stipules, insignificant leaf-like appendages of the leaf-base. If the blade of leaf is removed, these stipules will often become very much enlarged and take over the duties of the destroyed leaf blade. A similar change into a flat blade has been observed in the slender tendrils which terminate the leaf in certain plants, like the pea, when the leaflets have been removed. In some species of ferns, the spore-bearing leaves are much smaller than the large sterile leaves, and normally develop comparatively little green tissue. If, however, the sterile leaves, which are the principal photosynthetic organs, are removed while young, the sporophylls which arise later will assume more or less perfectly the character of the amputated fronds. By cutting back the leafy stem of a potato plant, the underground shoots which normally develop into the tubers, will appear above the ground and develop into leafy shoots, while if the young tubers are constantly removed, the reserve food which would normally be stored up in these will accumulate in tubers formed above the ground from some of the aerial shoots. A familiar case of substitution is that occurring in many conifers. If the leading shoot of a pine or fir is destroyed, a lateral shoot below it will usually grow upward and take its place. This accelerated growth and change of position are supposed to be due to the diverting of the flow of nutritive matter from the destroyed apical shoots, to one of the lateral ones.

**Klebs' Experiments on Formative Effects of Stimuli.**—The various formative factors, light, heat, food, etc., have already been sufficiently discussed and will not be dwelt upon here at length, but it may be worth while to refer briefly to a few cases where the formative effects of some of these stimuli have been critically studied. Klebs for several years has been investigating the direct causes affecting the character of plant structures, and the results of his studies are extremely interesting and valuable. Especially instructive are some of his studies upon the lower organisms, whose simplicity makes it easier to judge the direct effects of the stimuli employed in the experiment. Klebs showed that it is possible for the experimenter to control almost absolutely the character of the development of the plant. By the employment of certain stimuli, e.g., light of varying intensity or color, nutritive media of different kinds, etc., the plant can be forced to develop in almost any way the experimenter may select.

Reproduction of any type can be induced, or the reproductive activity may be entirely suppressed. Klebs has later extended his studies to the higher plants, where, owing to the greater complexity of the organism, the formative factors are not nearly so clearly evident. Nevertheless, in these higher plants, also, he has shown that it is possible to control to an extraordinary degree the development. By varying the character of the light, tem-

perature, and nutritive conditions, he showed that not only the habit of the plant might be greatly changed but the color and size of the flower, and sometimes even the number of different parts, might be altered very much; so that in the case of a species of house-leek (*Sempervivum*), for example, the differences in the flowers were much greater than those between some of the species of the genus.

Klebs' conclusions from his studies are that variability and inheritance are the results of physiological changes entirely and there is no necessity for assuming the existence of definite formative structures or protoplasmic units, pangenes, or determinants, etc. Unfortunately the possibility of hereditary transmission of the changes induced by environmental conditions, has not yet been investigated as fully as could be wished.

### CONCLUSION

**No Single Theory Satisfactorily Explains All the Facts of Evolution.**—From a study of the behavior of plants in a state of nature, as well as under experimental conditions, it is certain that no one of the many theories that have been advanced can explain satisfactorily all of the phenomena associated with the evolution of the vegetable kingdom. There is no question that mutations or discontinuous variations do occur, and that these may be the beginning of new species is exceedingly proba-

ble; but that there is necessarily a radical difference between mutations and fluctuating variations has not been satisfactorily proven; and the fact that by artificial selection of slight differences new forms may arise, makes it highly probable that these fluctuating variations may also be potent in species forming under natural conditions. The occurrence of well-established natural hybrids makes it practically certain that new species sometimes arise directly by the crossing of two well-marked species.

It also becomes more and more evident that the plant organism is extremely plastic, and readily influenced by changes in the environment, and that the results of such changes may be transmitted to the offspring. The generalized character of the tissues of even the highest plants, shown especially by the study of regeneration, does not support the theory of a special germ-plasm, directly associated with the transmission of hereditary characters. The view that the laws of heredity are exclusively physiological is probably too extreme, but on the other hand it does not seem necessary to assume the presence of an infinity of morphological units, "gemmules," "determinants," etc. It is almost certain that the protoplast does contain many permanent, but invisible, organs, comparable to the nucleus and chromatophores, but the development of the organism probably depends quite as much upon the potentialities of these to respond to stimuli, as to their actual form or chemical structure. Whatever

factors may be shown to cause the appearance of new forms, or incipient species, the survival of these must depend upon natural selection.

In the history of both the vegetable and animal kingdoms, the most important event was the deserting of the primitive aquatic environment for life in the air. Fungi, Ferns, and Seed-plants on the one hand; Insects, Birds, and Mammals on the other, prove the superiority of the land over the sea, as a field for the work of evolution.



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